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LIBERATION OF ORGANIC MATTER BY ROOTS OF GROWING PLANTS

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CONTENTS

PAGE

Review of literature concerning loss of nitrogen by growing plants... 7
Object of the present experiments... 14
Method used... 14
Seed sterilization... 15
Preparation of the flasks... 16
Nutrient solution... 16
Setting of the plants... 17
Harvesting the plants... 17
Analysis of nutrient solutions and residues in bottom of flasks... 17
Tests for the presence of organic nitrogen in nutrient solutions in which plants of several kinds had grown... 18
Organic nitrogen present in nutrient solutions at successive stages in the growth of maize... 23
Total organic matter present in nutrient solutions in which maize plants had grown... 31
Reducing and oxidizing substances liberated by plant roots... 34
Review of literature... 35
Tests for reducing and oxidizing substances liberated by plant roots... 36
Reducing substances... 36
Reduction of nitrates... 37
Oxidizing substances... 39
Possible coexistence of oxidizing and reducing substances... 40
Nature of oxidizing and reducing substances... 40
Summary... 40
Bibliography... 43

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T. L. Lyon and J. K. Wilson

In the course of an investigation under way at this station, it became desirable to know whether organic matter, particularly that of a nitrogenous nature, is liberated by the roots of growing plants, at least of the plants commonly raised on farms in this region. Numerous investigations conducted elsewhere have shown that nitrogen is lost by certain plants during the late stages of growth, particularly about the ripening period. There seemed to be a question, however, whether this nitrogen escaped from the leaves or the roots, and it had never been shown to be in the form of organic matter. The previous investigations had, indeed, not touched on the question of the loss of organic matter by growing plants, and aside from its bearing on the investigation in hand this appeared to be a matter of some scientific interest.

A closely related question is the possible liberation of reducing or oxidizing substances by the roots of growing plants. There had previously been some investigation of this subject, but since the experiments on the liberation of organic matter furnished exceptionally good opportunities for making the tests for catalysts it was decided to try to obtain some information to supplement the previous work.

REVIEW OF LITERATURE CONCERNING LOSS OF NITROGEN FROM GROWING PLANTS

A large amount of work has been reported showing the percentage of the various nutritive elements found in crops at certain stages of growth. Less work has been done, however, on the actual weight of nutrients in plants during their growth and maturity.

The work of Wilfarth, Römer, and Wimmer (1906) was concerned with the assimilation of the elements of nutrition by plants during different periods of their growth. This investigation extended over a period of about eight years. The experiments included both field and pot work, the former with barley, spring wheat, and potatoes, and the latter with

barley, peas, potatoes, and mustard. The plants were harvested at different stages of growth. These plants were carefully divided into their component parts — roots, stems, ears, and so on — and were dried, weighed, and analyzed. The results as stated below are based on pounds of nitrogen in the crop.

The barley was planted on March 30 and the cuttings were made on May 29, June 17, July 3, and July 27. The plant parts were separated and grouped into aboveground parts and underground parts. Separate analyses were made of stems, green leaves, yellow leaves, ear stalks, awns, straw, grain, roots, and stubble. Total weights of nitrogen showed that this nutrient was present in its greatest amount on June 17 (presumably when the plants were in bloom) and that the mature cutting of July 27 had lost 25 per cent of the total nitrogen.

The wheat was planted on April 23 and was harvested on June 22, July 14, August 5, and August 28. The methods used were the same as for barley. In the case of the wheat, the nitrogen was found in its greatest amount in the third cutting, on August 5, and the mature crop showed a loss of about 20 per cent of the total nitrogen.

The potatoes were planted on April 28 and analyses were made of the various parts of the plant. Four different harvests were gathered as the crop was maturing. The results were quite different from those with barley or with wheat. In this case the greatest amount of nitrogen was found in the last harvest, which represents the crop gathered in October.

The barley was planted on April 20 in sand in pots, and was watered with nutrient solutions. Quadruplicate cultures were grown in the greenhouse. On May 11 stems had commenced to show. The first harvest was made on May 24, the second on June 1, the third on June 12, the fourth on June 25, the fifth on July 20. The harvest consisted of both roots and tops. In one series the greatest weight of nitrogen was found on June 25, in the other three on June 12. From these dates on to maturity there was a loss of total nitrogen ranging from 9 to 26 per cent.

The peas were planted and tended in a similar manner to the barley, with the same dates for planting and harvesting. The weight of nitrogen in the harvested crops was greatest on June 25 in three cases, and in the fourth case at the last harvest. The decrease toward maturity in the three cases ranged from 9 to 30 per cent.

The potatoes were grown in turf and sand in the greenhouse. Applications of fertilizer were made so that plant nutrients would not be deficient. Harvests were made on June 12, June 30, August 7, and September 14. The plant parts were divided into foliage and tubers. The figures for weight of nitrogen show that there was a constant decrease of this constituent in the foliage after the first harvest, altho there was a constant increase in the weight of the tubers. The total plant, however, had its greatest amount of nitrogen on August 7, with a decrease of 6.46 per cent thirty-eight days later.

Pots containing 5.3 kilograms of dry earth received fertilizers to stimulate growth of plants and to furnish an abundant supply of nutrients. The seeding of mustard was done on May 7, and subsequently all pots contained six plants. The experiment was run in duplicate. The mustard was harvested, first, on the appearance of the first pods, second, when the formation of seed was complete, and third, at maturity. Analysis of the total plant only was made. The total nitrogen was greatest when the formation of seed was complete. The loss at the third harvest was about 10 per cent of the total nitrogen.

With the intention of verifying the results obtained by Wilfarth, Römer, and Wimmer, André (1912) cut barley at five different stages of growth from equal areas of land and analyzed the dry harvest. The cuttings were made (1) when the heads began to show, (2) when the barley was in bloom, (3) when seed began to form, (4) at the mature stage, and (5) beyond the ripe stage. The figures for total nitrogen show 7.023 grams at the first stage, 8.693 at blooming, 10.422 when the fruit was forming, 12.389 at maturity, and 10.360 at the last harvest.

The object of an experiment by Ramsay and Robertson (1918) was to determine the relative proportions of each of the principal nutrient elements contained in the plant at various stages of growth. They grew potatoes in soil in boxes containing about 130 pounds of well-drained and fertilized soil. Approximately the same weight of seed was put in each box. The first harvest was gathered on January 29, thirty-three days after brairding, the second on February 25, the third on March 26, and the last on April 30. At the first three harvests complete recovery of tops and roots was made. The last harvest was more difficult and about 30 per cent of the roots were lost. Cropping, harvesting, and analyzing were done in duplicate in each case. The total nitrogen contained in a 20-ton crop of

potato plants at various stages of development was 69 pounds at the first harvest (thirty-three days), 241.3 pounds at the second harvest (fifty-eight days), 306.7 pounds at the third harvest (eighty-nine days), and 319 pounds at the fourth harvest (one hundred and twenty-four days). There was a constant assimilation of this important element.

Hay was cut by Crowther and Ruston (1911–12) from uniform areas of a crop of grass which had been seeded the previous spring. The grass seed consisted of a mixture of perennial rye grass, Italian rye grass, white clover, trefoil, alsike, English single-cut cow grass, Chilean red clover, and rib grass. The first cutting was made when the rye grass was in full flower. A good growth of leguminous plants showed underneath. The second cutting was made when the rye grass was forming seed and the clovers were beginning to flower. At the third cutting the grasses were ripening and the clovers were in full bloom, while the fourth and last cutting was made when the crop was decidedly ripe. Analysis of the crops showed the greatest total weight of nitrogen to be present at the third cutting, or when the grasses were ripening and the clovers were in full bloom. In the last cutting there was a loss of 25 pounds of nitrogen to the acre.

The work was repeated the following year, but with barley as the crop. The seed was drilled on May 12. Cuttings were made on June 9, June 23, July 7, and July 21, but the stages of growth reached on these dates were not noted. The changes with advancing age as to nitrogen were similar to those observed in the preceding year with grasses.

The changes in chemical composition of the timothy plant during growth and ripening, with comparative studies of the wheat plant, are recorded by Trowbridge, Haigh, and Moulton (1915). Timothy plants, cut from uniform areas, represented the following stages of growth: (1) about one foot high in rapid growth; (2) no heads showing; (3) no stalks in bloom but beginning to head; (4) in full bloom; (5) just out of bloom and seed formed; (6) seed in dough; (7) seed fully ripe; (8) growth the following spring not yet started but leaves green. The plant parts of the samples thus collected were divided into heads, stalks and leaves, hay, and stubble and bulbs. The amounts of the various nutrients determined were recorded in total pounds to the acre. Data from these plants were collected for one year only. The figures for weight of nitrogen showed that there was a gradual increase in this constituent in heads from

all plots. In the stalks and leaves, the nitrogen was found in greatest amounts in two cases when the plants were just out of bloom and the seed was formed, and in the third case when no stalks were in bloom but the plants were beginning to head. In the hay the greatest weight of nitrogen was found when the seed was all in dough. In the stubble and bulbs the greatest amount of nitrogen was present when the seed was fully ripe.

The comparative studies with wheat represent two areas from the same field. The stages of development were: (1) plants green and in bloom; (2) seed formed and in milk; (3) seed in dough; (4) seed fully ripe. The plant parts of the samples were divided into heads, stalks and leaves, plants above ground, and roots and stubble. The figures for nitrogen found in the heads showed a steady increase in this nutrient thruout all the stages. With stalks and leaves there was a constant loss of nitrogen after the first stage as the plant approached maturity. In the plants above ground there was an increase of nitrogen to the seed-in-dough stage and a considerable loss in the fully-ripe stage. Roots and stubble contained their greatest weight of nitrogen at the seed-in-milk stage. If the total plant is considered, the nitrogen reached its greatest amount when the seed was in the dough stage.

The influence of advancing maturity on the composition of timothy was reported by Waters (1915). Results were obtained for five years of investigation, but the results are complete for only three of these years. Uniform areas were harvested at five different stages of growth: (1) when the plants were in full head; (2) when the plants were in bloom; (3) when the seed had formed; (4) when the seed was in dough; (5) when the seed was ripe but not shattered. The greatest weight of nitrogen was found in three of the trials when the plants were in full bloom, and in the other two trials when the seed had formed. The fluctuation in loss of nitrogen between the stages when it was at the maximum and when it was fully ripe ranged from 12 to 38 per cent.

Schulze (1904) cut 100 plants of rye and collected the roots for examination. The cuttings were made forty days after drilling, which was on September 20. On April 22 a second cutting was made. The plants at this stage were very green. On May 20 a third cutting was made. The plants now were in the boot stage. The fourth cutting was made on June 16 and the plants were just thru blooming. The weight of nitrogen

in these stages was as follows: first cutting, 0.153 gram; second cutting, 1.225 grams; third cutting, 2.723 grams; fourth cutting, 2.713 grams.

With wheat only three harvests were made: the first was thirty-seven days after drilling, which took place on September 23; the second was on April 22, and no heads were showing at this date; the third was on June 16, when the plants were thru blooming. The nitrogen in 100 plants was as follows: first period, 0.132 gram; second period, 0.596 gram; third period, 1.802 grams. No later analyses are given, and thus it is not clear whether there was a loss in weight of nitrogen after the blooming period.

Le Clerc and Breazeale (1909) state that the loss of nutrients from plants may be explained in one of three ways: (1) by the backward flow of the salts of the plant juices thru the stems and roots to the soil; (2) by the decay or dying and falling off of leaves; or (3) by the action of rain, dew, wind, and other climatic agencies. Or there may be a combination of all these causes to a limited extent. In support of the third possibility, these investigators conducted experiments designed to imitate these climatic agencies. Barley plants were grown in soil contained in Wagner pots, and no water was allowed to come in touch with the aboveground parts during the growing period. Just at the heading period the whole plant was harvested, placed in a large evaporating dish, and soaked with water for several minutes. After drying, this operation was repeated. The plants were then dried and analyzed. The results show that 1.6 per cent of the entire content of nitrogen was lost on washing.

Wheat plants were harvested at three periods of growth — bloom, early ripeness, and full ripeness. The plant parts were divided into stems and straw, and heads. They were separately washed or soaked for from five to ten minutes. The wash water was analyzed, as were also the dried stems and straw and the heads. The results show that at bloom 1.4 per cent of the nitrogen was washed out, while at full maturity 7 per cent was found in the wash water.

Results were obtained also from apple twigs. Two twigs containing green leaves were gathered and washed for a few minutes with distilled water. They were then set aside, with their butt ends immersed in water, until the leaves were unquestionably dead, when they were again washed and analyses were made of both washings and residues. The results of the analyses showed that thru the action of water about 3 per cent of nitrogen had been washed out.

Two pots of wheat were kept in the greenhouse until the wheat was completely ripe. They were then placed out of doors, where they were subjected to four rainfalls on separate days. The pots were so arranged that the washings were caught in a tray. These washings, equivalent to about one inch of rainfall, dissolved from the plant 27 per cent of the nitrogen as well as other nutrients.

Two oat pots were placed out of doors as were the wheat pots. The plants were about eight inches high. They were allowed to grow in this position until they were ripe. They were exposed to three rains during this time. The leachings contained 2 per cent of the nitrogen, as well as other nutrients.

In two pots of potatoes, the aboveground parts were washed with 2.5 quarts of water in a very fine spray. This was done when the plants were twenty-four inches high, when they were beginning to ripen, and when they were completely ripe. The leachings and the plant parts above ground were analyzed. The results show that, due to the action of washing, 7.5 per cent of the nitrogen was washed out.

Jones and Huston (1914) report the composition of the maize crop at stages corresponding in the main with those at which the crop would be used for practical purposes, such as soiling, ensiling, and grain production. Conditions of uniformity were maintained as nearly ideal as it was possible to have them. In order to insure adequate moisture, the field was irrigated when necessary so as to provide not less than one inch of water every week. The soil was in a good state of fertility. Analyses were made as follows: (1) when the plants had six leaves, June 16; (2) when the plants were about four feet high, July 24; (3) when tassels began to form, August 6; (4) when the maize was fully pollinized, August 28; (5) when the plants were in the medium milk stage, with the pollen all shed and the silks brown, September 10; (6) when the kernels were glazing, September 24; (7) when the kernels were hardening, this being the ensiling stage, October 1; (8) when the maize was ready to put into shock, October 8; (9) when the maize was fully cured and ready to be stored, November 12.

The samples represented the crop cut at the soil level. Data for weight of nitrogen showed a gradual increase from the first analysis to October 8, the amount at first being 0.28 pounds an acre and increasing to 110.6 pounds on the last-named date. At the last analysis, on November 12,

which represented samples left in the field and in the shock, for the former a loss of about 23 pounds was shown, while for the latter a slight gain was reported. This loss of nitrogen when the plants were left in the field after October 8 was from both ears and stalks. In the former there was a loss of 9.2 pounds in the field and a gain of 7.6 pounds in the shock; in the latter there was a loss of 15 pounds in the field and a loss of only 2.1 pounds in the shock.

Taking the results of these investigations as a whole, there appears to be in nearly all cases a loss of nitrogen from grass and small grains at some time between the period of full bloom and complete maturity. In maize this occurs if the plants are allowed to ripen when connected with the roots, but potatoes showed no loss of nitrogen in the Bernburg and Australia experiments, and only a small loss in those of Le Clerc and Breazeale.

OBJECT OF THE PRESENT EXPERIMENTS

The experiments herein described had two more or less distinct objects. The first was to ascertain whether growing plants liberate organic matter, and, if they do, to determine at what stage of growth this takes place and what relation it bears to the absorption of nitrate nitrogen by the plant. The second object was to detect, if possible, the presence of reducing and oxidizing ferments in the nutrient solutions in which the plants used for the first investigation were grown.

METHODS USED

The plants used in these experiments were grown in water culture. This was done in order that an intimate study might be made of the plant as it grew and the solution as it was being drawn upon by the plant for various nutrients, especially nitrogen. Since a number of organic bodies may be given off by the developing plant, these may not be present when the nutrient solution is analyzed if it is allowed to become infected with molds or bacteria. Therefore, in order that this solution should represent the action of the plant alone, a method for growing the root system in contact with the nutrient solution without infection was used. This method has been published, together with data showing its reliability (Wilson, 1920). A description of the method follows.

SEED STERILIZATION

Seeds were rendered sterile by the calcium hypochlorite method as employed by Wilson (1915). After disinfection the seeds were planted on a sterile medium, from which, after germination, the plants were transferred to the permanent position. The solid medium for the germination was usually composed of the same ingredients as were used in the large containers, from which the plants eventually drew their nutrients, with from 1 to 1.5 per cent of agar. The agar was used in order that contaminations might be detected before the plants were transferred to their permanent position. This medium was made in sufficient quantity to meet the requirements and was distributed into large test tubes.

Since the roots of most plantlets spread out in a lateral direction, thus making it difficult to transplant them quickly and conveniently, some device was needed which would direct the root growth in a vertical direction. To accomplish this there was placed in each test tube a short piece of glass tubing, 25 by 50 millimeters in size (fig. 1, *e*). A sufficient quantity of the medium was put into the tube to cover all but about 15 millimeters of this glass tubing. After sterilization of the medium the sterile seeds were dropped onto it, where they germinated and produced rootlets for subsequent use. When the roots

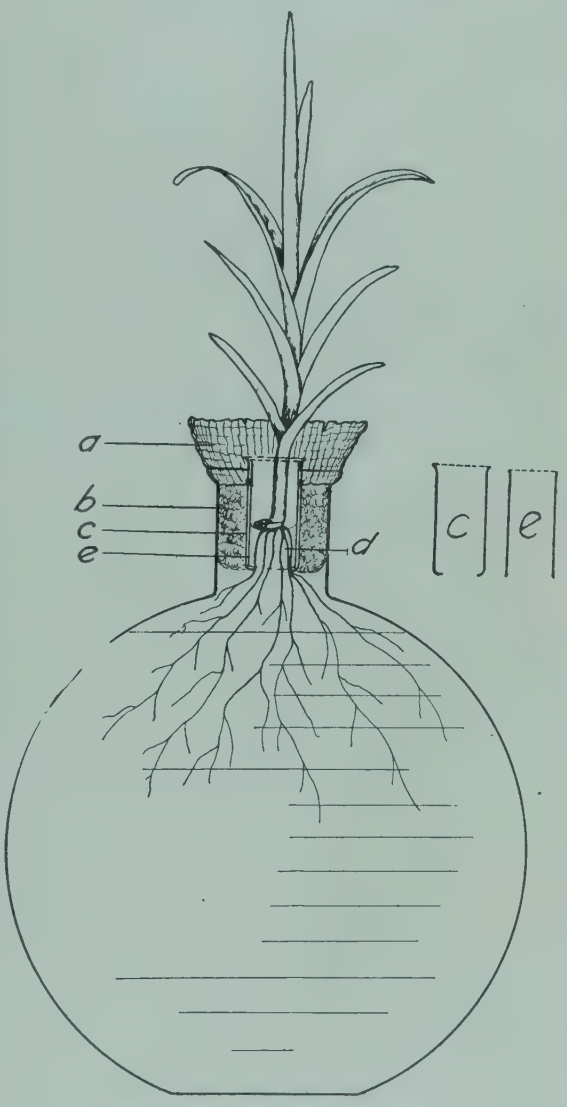

FIG. 1. DEVICE FOR GROWING LARGE PLANTS IN STERILE MEDIA

a, Cheesecloth; *b*, cotton wool; *c*, outside tube into which *e* slides; *d*, agar carried over from test tube with plantlet; *e*, tube in which seed germinates

had developed and passed thru the agar to the bottom of the glass tube, the plantlets were transferred. The tube (fig. 1, *e*), with agar and plantlets, was lifted out of the test tube and set into the mouth of the prepared flask. This was accomplished with sterile forceps.

PREPARATION OF THE FLASKS

The flasks used were in most cases of 8-liter capacity, altho some held 12 liters. As much of the nutrient solution was put into each flask as could be sterilized. A piece of cloth was stretched over the mouth, and a hole just large enough to permit the insertion of a piece of tubing from 28 to 30 millimeters long (fig. 1, *c*) was cut in the cloth. This tubing (*c*) was just large enough to allow the plant and its tubing (*e*), described above, to telescope into it.

The lower end of the tube (*c*) was slightly constricted, to prevent the inner tube (*e*) with the plant from going too far into the flask. Enough cotton (*b*) was wrapped around the tube to hold it firmly in place when it was pushed into the mouth of the flask. The upper end of the tubing was adjusted so that it came about even with the top of the flask. The lower end extended below the cotton and the cloth (*a*), so that when the flask was full of liquid the liquid would just touch the tubing but not the packing. Each flask was then covered with a large beaker. The inverted beaker was large enough to leave some space for the growing plant.

Since there was need for more solution in the flask than could be sterilized in it, an extra amount was prepared which could be poured thru the opening that was left.

NUTRIENT SOLUTION

The nutrient solution had the following composition:

Calcium nitrate, $Ca(NO_3)_2+4H_2O$	2.70 grams
Magnesium sulfate, $MgSO_4+7H_2O$	0.60 gram
Potassium chloride, KCl	0.75 gram
Potassium dihydrogen phosphate, KH_2PO_4	1.50 grams
Ferric sulfate, $Fe_2(SO_4)_3$	0.05 gram
Distilled water to make	1000 cubic centimeters

This was designated as the full nutrient solution. In most cases of actual use it was diluted to ten times this volume. In earlier work it had been noted that certain plants, especially maize, tend to become chlorotic

before maturity. By painting the blades with a ferric chloride solution, it was found that this chlorosis was due to a deficiency of available iron. Therefore about 0.5 gram of ferric phosphate was added to each container before sterilization.

SETTING OF THE PLANTS

Before the plantlets were set into the mouth of the flasks they were thoroly examined for contamination. Only the very best plantlets were used, and if properly handled they suffered no setback. In case the plantlets were large enough when placed in the flasks, they were wrapped in sterile cotton and the beaker was removed. In other cases several days were required for the plants to become large enough, and in this event the beaker was left on.

HARVESTING THE PLANTS

The plants were harvested in all stages of growth, as is shown by figures 5 to 9. The harvesting process consisted in bringing flask and plant to the laboratory, and, in most cases, first making a photograph and subsequently opening the flask by removing the plant and the cotton packing. When this was done the solution was examined for infection, which was determined by plating about 10, 5, 1/10, and 1/100 cubic centimeters. The medium used in the plates contained, in addition to peptone and beef extract, some form of sugar, usually glucose. The plates were incubated at from 20° to 25° C. for a week, or longer in case no infection was noted. The results reported in the subsequent data herein were obtained from the platings in which no infection was found, and these flasks were considered to be sterile.

ANALYSIS OF NUTRIENT SOLUTIONS AND RESIDUES IN BOTTOM OF FLASKS

The presence of nitrite nitrogen was determined by Ilosvay's modification of Griess' test, described by Treadwell (1915).

A qualitative test for the presence of nitrate nitrogen was made by the diphenylamine method (Withers and Ray, 1911). When it was present, the total quantity was determined by the phenoldisulfonic-acid method, slightly modified by the addition of 5 drops of a 0.5-per-cent solution of Na_2CO_3 before evaporating to avoid any loss of nitrogen which might be

FIG. 2. OAT PLANT GROWN IN STERILE SOLUTION FOR 105 DAYS

(Table 1, serial no. 1272)

present in the form of HNO_3. (The quantity of soluble organic matter in the plant solutions was not great enough to interfere with the proper nitration of the phenoldisulfonic acid.)

Ammonia was determined by direct nesslerization.

Organic nitrogen in the plant solutions was determined according to the method described by the American Public Health Association (1905).

The total organic matter in the solutions was determined by evaporating 100 cubic centimeters of the filtered solution and igniting the residue thus obtained at dull red heat. The loss on ignition was reported as organic matter.

The dry weight of the deposit in the bottom of each flask was ascertained by transferring it to a filter, drying it at 110° C., and weighing it, the weight of the dry filter being subtracted from the total weight.

The amount of organic nitrogen in the deposit in the bottom of each flask was found by transferring the filter and contents from the previous determination to a Kjeldahl flask, digesting by the Gunning method, neutralizing the excess acid with ammonia-free Na_2CO_3, and distilling off the ammonia, which was nesslerized.

TESTS FOR THE PRESENCE OF ORGANIC NITROGEN IN NUTRIENT SOLUTIONS IN WHICH PLANTS OF SEVERAL KINDS HAD GROWN

Several different kinds of seeds were germinated under aseptic conditions, and were transplanted, in the manner described, to flasks containing the usual nutrient solution of one-tenth strength. The manner of growth of the plants in these flasks is shown in figures 2 to 4.

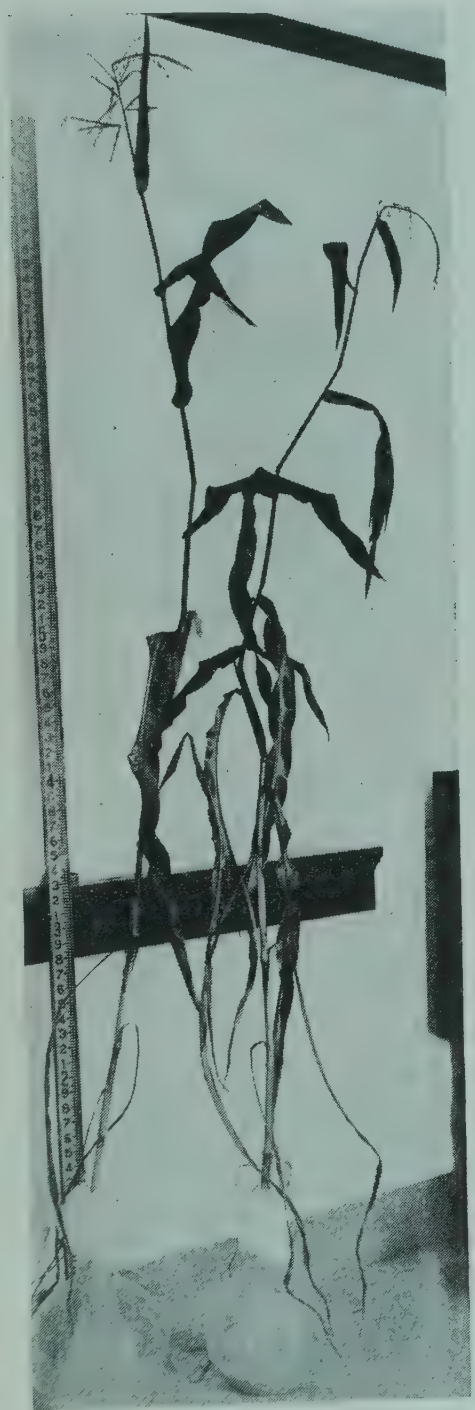

FIG. 3. MAIZE PLANTS GROWN IN STERILE SOLUTION FOR 189 DAYS

(Table 1, serial no. 1303)

FIG. 4. PEA PLANT GROWN IN STERILE SOLUTION FOR 139 DAYS

(Table 1, serial no. 1280)

In one flask the usual nutrient solution was not employed, as it was desired to ascertain whether a leguminous plant grown in a solution containing no nitrogen would liberate nitrogenous matter in the solution in appreciable quantities. The flask used for this purpose was pea flask no. 1302, in which the nutrient solution was composed of 1.5 grams KH_2PO_4, 1 gram $CaCl_2$, 0.07 gram Na_2SO_4, and 0.5 gram $Fe_2(PO_4)_2 + 8H_2O$; the flask was then filled with sterile tap water, the $Fe_2(PO_4)_2 + 8H_2O$ remaining largely undissolved.

After the contents of the flasks were sterilized and the young plants transferred, the cultures were taken to the greenhouse, where they remained for various periods. It was not intended to make any systematic study of the relation of the stage of growth to the quantity of organic nitrogen in the solution at harvest. This would have been impossible under the circumstances, for the plants were set out at different times and, since conditions affecting plant growth vary greatly in the greenhouse at different seasons of the year, no comparison of this kind could be attempted. The same difficulty would obtain in case a comparison of different plants was desired, except in the case of such plants as were placed in the greenhouse at about the same time.

When it was decided to harvest a plant, the flask was brought to the laboratory, and, after a photograph had been taken, the plant was removed from the nutrient solution and the dry matter and nitrogen were determined in the entire plant including the roots. A plating of the nutrient solution was made to determine whether the solution was sterile. The presence of any molds or bacteria thus detected excluded from the experiment the flask so contaminated.

The volume of liquid remaining in the flask was measured, and determinations were made of the nitrate nitrogen remaining in the solution, the ammonia nitrogen, if any, and the organic nitrogen present in soluble form. The deposit at the bottom of the flask was collected and a determination was made of the organic nitrogen contained in it. The reason for ascertaining the quantity of nitrate nitrogen remaining in the solution was merely to observe whether the presence or absence of this form of nitrogen affected the liberation of organic nitrogen by the plant.

A small quantity of nitrogen was contained in the germinated seed and plantlet placed in the flask, but there was no way by which this nitrogen

TABLE 1. FORMS AND AMOUNTS OF NITROGEN PRESENT IN SOLUTIONS IN WHICH PLANTS HAD GROWN

Kind of plant	Maize	Oat	Pea	Pea*	Maize	Vetch
Serial no.	1259	1272	1280	1302	1303	1308
Date of setting plant in flask	Dec. 1	Dec. 29	Dec. 9	Dec. 9	Dec. 1	Jan. 20
Date of removing plant from flask	April 1	April 11	April 26	April 26	June 7	June 12
Growing period (days)	122	105	139	139	189	144
Dry matter in plant (milligrams)	11,367.8	4,089.0	6,823.0	.....	48,490.0	18,050.0
Nitrogen in plant (milligrams)	248.9	151.0	231.5	43.6	472.3	344.9
Volume of solution at harvest (cubic centimeters)	9,850.0	7,320.0	4,510.0	6,815.0	6,950.0	2,290.0
Condition of solution	Sterile	Sterile	Sterile	*B. radicicola*	Sterile	Sterile
Nitrogen in solution at harvest in form of						
NO_3 (milligrams)	241.9	198.3	89.6	None	None	None
NH_3 (milligrams)	2.7	Trace	Trace	2.0	6.3	None
Organic matter (milligrams)	13.4	18.3	3.6	2.0	3.4	4.4
Organic nitrogen in deposit at bottom of flask (milligrams)	0.8	0.5	0.2	0.7	0.6	1.0

* The nutrient solution in which this pea plant was grown contained no combined nitrogen at the beginning of the experiment.

could be transferred to the nutrient solution except thru the roots, as the seed did not come in contact with the solution at any time.

The data for this experiment are presented in table 1. The figures give some definite information regarding the presence of organic nitrogen in the substratum in which these plants grew and which contained only inorganic nitrogen at the time when the young plants were set out. Of the plants used — oats, peas, maize, and vetch — all liberated organic nitrogen, which was found both in the solution and in the deposit at the bottom of the flasks. The quantity of organic nitrogen in the solution was always several times as much as that in the deposit.

The organic nitrogen in the deposit at the bottom of the flasks is probably the result of sloughing off of the root cells, as is indicated by the presence of plates of cells in the deposit. It is possible also that a part, at least, of the nitrogen in solution is liberated from the plant cells in the same way. There is no direct evidence that the nitrogenous matter is liberated in any other way, but it is perhaps questionable whether the quantity found in solution, especially during the early stages of growth, could all have come from detached cells. That these cells are alive and remain so for a considerable time has been noted by Knudson (1919).

Organic nitrogen appeared in the solution before the nitrates were all removed. It is evident that organic nitrogen is liberated by these plants in the early stages of their growth and not exclusively at the period between full bloom and maturity. That only the loss of nitrogen in later growth was noticed in the field experiments previously reviewed was doubtless due to the fact that the plants were absorbing little nitrogen at that stage and were liberating it more rapidly than they were absorbing it.

The quantity of organic nitrogen liberated under field conditions may not correspond to that obtained in these experiments, as under the conditions of the experiments there was no removal of organic matter by organisms other than the plant, while in the field there would presumably be conversion of the organic nitrogen into ammonia and nitrates.

The pea plant that grew in a solution without the addition of combined nitrogen, liberated organic nitrogen into the solution in which it grew. The growth was by no means as vigorous as that of the pea plant which was furnished with nitrate nitrogen, and the plant itself contained only about one-fifth as much nitrogen as did the other pea plant, but it liberated more than half as much organic nitrogen.

ORGANIC NITROGEN PRESENT IN NUTRIENT SOLUTIONS AT SUCCESSIVE STAGES IN THE GROWTH OF MAIZE

In order to ascertain how the stage of growth of maize plants affects the quantity of organic nitrogen found in the nutrient media, a series of flasks containing nutrient solution were prepared in the usual way and a young plant was set in each flask. The flasks were placed in the greenhouse on December 24, 1915. They were allowed to remain there until the time when they were to be brought to the laboratory for analysis of the plants and the contents of the flasks. The first flask was opened on March 4, 1916, and the others were opened at intervals of a number of days until May 24, 1916, when the last one was opened. The interval between the opening of the first and that of the last flask covers a period of growth between the pre-tassel stage and maturity (figs. 5 to 9).

The maize plants grew well and most of those that were old enough at harvest bore ears. The variety used was a pop corn which under normal conditions does not grow very tall. Data regarding all of the flasks the contents of which were sterile at harvest are given in table 2. All of the contaminated flasks except one were discarded in presenting the results. The one exception was made because it fell in what would otherwise have been a wide interval between the dates of harvest. It also represented the condition of most of the contaminated flasks, which did not appear to be materially different from the sterile flasks in respect to the quantity of organic nitrogen present in the nutrient solution.

The data in table 2 are consistent in showing the presence of organic nitrogen in all solutions in which plants grew. This organic nitrogen appeared at all stages in the growth of the plants, but there seemed to be a tendency for it to decrease in amount with progressive stages in the life of the plant, and especially about the time when the plant approached maturity, at which stage there was a very decided falling off in the quantity present.

The organic nitrogen in the deposit at the bottom of the flask did not show any decided tendency to vary in amount with the successive stages of plant growth. The amount present was uniformly smaller than that in the solution. In the bottom of the flask there could usually be found plant cells, indicating the sloughing off of root caps and root hairs. This suggests a possible source of at least a part of the organic nitrogen in

FIG. 5. MAIZE PLANT 71 DAYS OLD

FIG. 6. MAIZE PLANT 82 DAYS OLD
(Table 2, serial no. 1250)

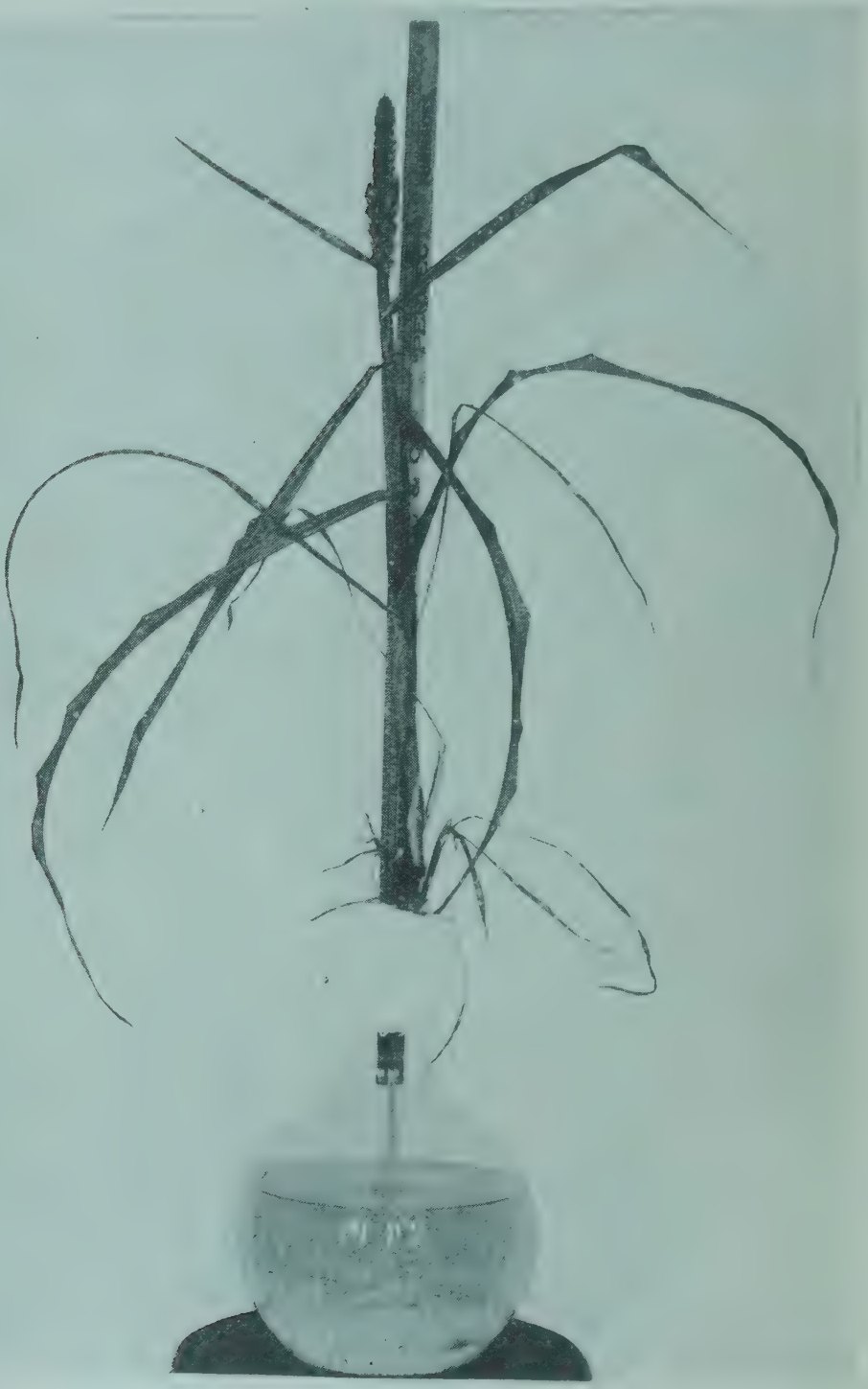

FIG. 7. MAIZE PLANT 91 DAYS OLD
(Table 2, serial no. 1253

Fig. 8. MAIZE PLANT 96 DAYS OLD
(Table 2, serial no. 1256)

Fig. 9. Maize plant 111 days old
(Table 2, serial no. 1275)

TABLE 2. FORMS AND AMOUNTS OF NITROGEN PRESENT IN SOLUTIONS AT SUCCESSIVE STAGES IN THE GROWTH OF MAIZE

Kind of plant	Maize	Maize	Maize	Maize	Maize	Maize	Maize	Maize
Serial no	1246	1250	1253	1256	1275	1286	1291	1295
Date of setting plant in flask	Dec. 24	Dec. 24	Dec. 24	Dec. 24	Dec. 24	Dec. 24	Dec. 24	Dec. 24
Date of removing plant from flask	March 4	March15	March24	March29	April 14	May 3	May 17	May 24
Growing period (days)	71	82	91	96	111	130	144	151
Dry matter in plant (milligrams)	8,572.0	12,518.9	17,164.4	20,246.7	36,570.4	42,387.5	44,591.6	33,804.5
Nitrogen in plant (milligrams)	Lost	381.3	324.5	364.6	308.3	332.4	476.3	324.9
Volume of solution used by the plant (cubic centimeters)	1,370.0	2,040.0	2,500.0	2,960.0	5,705.0	6,455.0	8,240.0	5,710.0
Condition of solution	Sterile	Sterile	Sterile	Contami-nated	Sterile	Sterile	Sterile	Sterile
Nitrogen in solution at harvest in form of								
NO_3 (milligrams)	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NH_3 (milligrams)	0.0	0.0	2.4	0.0	4.0	0.5	0.7	7.0
Organic matter (milligrams)	13.4	5.8	10.5	10.6	9.0	0.6	0.6	1.4
Organic nitrogen in deposit at bottom of flask (milligrams)	.....	0.9	1.2	0.6	0.9	Lost	0.4	1.0

solution and in the deposit, but whether it would account for all of the former may be questioned.

It was when the solution remaining in the flask was reduced to a rather small volume that the quantity of organic nitrogen in the solution fell decidedly. However, it did not appear that this was due to the saturation of the solution, as the large flask no. 1291, which contained 3700 cubic centimeters of solution at harvest, had no more organic nitrogen in the solution than did the smaller flask no. 1286, which contained only 1500 cubic centimeters of solution when opened.

It seems likely that the organic nitrogenous compounds are absorbed by the plant as it approaches maturity. This may be in order to establish equilibrium between the plant juices and the solution in which the roots are immersed. In the soil there would probably be a tendency for these organic nitrogenous compounds to undergo ammonification and nitrification, and, if conditions are favorable for these processes, there might be very little organic nitrogen in the soil solution at any time. Consequently, if there is a tendency to establish osmotic equilibrium there would probably be a much greater removal of organic nitrogen from a plant growing in soil than from one growing in a sterile solution.

Organic nitrogen appears in the nutrient solution before all of the nitrate nitrogen has disappeared, but the disappearance of nitrates is not a signal for the decided drop in organic nitrogen which occurs much later.

Previous investigations concerning the liberation of nitrogen from higher plants during growth have been conducted in two ways. One of these consisted in analyzing the plants from a measured area of land at certain intervals in the growth of the plants. Such experiments usually demonstrated that there was a loss of nitrogen from the plants between blossoming and ripening. Owing to the fact that the plants were absorbing nitrogen rapidly at earlier stages of growth, the income was greater than the outgo and consequently the earlier movement of nitrogen was not discovered. The other method, used by Le Clerc and Breazeale, in which the leaves were washed, showed a removal of nitrogen at each stage at which it was applied, but naturally the loss so occasioned would be rather small under natural conditions as it would occur only during periods of rainfall or heavy dew.

The movement of organic nitrogen from the plant into the soil solution would presumably be considerable, and possibly the cycle involving the absorption of nitrate nitrogen by the plant and its conversion into organic compounds followed by a return to the soil of a part of these compounds and a reconversion of the nitrogen into nitrates may be a very extensive one. What part it may play in the economy of the plant is at present only a matter of speculation. It may be that the liberation of this material is merely casual, while, on the other hand, it is conceivable that the substances so eliminated are more or less injurious to the plant and when exposed to the decomposing bacteria of the soil are destroyed and not reabsorbed. When liberated into a sterile solution they are not destroyed, and, being largely reabsorbed, they may exert a toxic effect on the plant, which never makes a perfectly healthy growth in these solutions even when it produces grain.

TOTAL ORGANIC MATTER PRESENT IN NUTRIENT SOLUTIONS IN WHICH MAIZE PLANTS HAD GROWN

The experiments previously described have dealt only with the forms of nitrogen present in solutions in which higher plants have grown. It would appear to be a matter of some interest to know something of the total quantity of organic matter in these solutions, and what proportion this organic matter may bear to the nitrogen present. For this purpose a number of flasks containing the usual nutrient solution of one-tenth strength were prepared and maize plants were grown in these in the customary way. It was planned to have a set of four flasks to be opened after the plants had grown for about two months, and another set of the same number of plants to be harvested when fully mature. Unfortunately, the flasks in the latter set were all found to be contaminated when opened, and for that reason the data furnished by these flasks are not considered to be of value and are not included in table 3, which gives the data for the first four flasks only:

TABLE 3. TOTAL ORGANIC MATTER AND NITROGEN PRESENT IN SOLUTIONS IN WHICH MAIZE PLANTS HAD GROWN

Kind of plant	Maize	Maize	Maize	Maize
Serial no	1	2	3	4
Date of setting plant in flask	May 1	May 1	May 1	May 1
Date of removing plant from flask	June 23	June 23	June 23	June 23
Growing period (days)	53	53	53	53
Dry matter in plant (milligrams)	17,266.4	23,076.4	24,058.5	20,443 0
Nitrogen in plant (milligrams)	357.1	327.4	400.0	365.8
Volume of solution at harvest (cubic centimeters)	5,875.0	4,155.0	3,855.0	4,870.0
Condition of solution	Sterile	Sterile	Sterile	Sterile
Total organic matter in solution at harvest (milligrams)	466.6	353.1	476.1	535.7
Nitrogen in solution at harvest in form of				
NO_3 (milligrams)	0.0	0.0	0.0	0.0
NH_3 (milligrams)	0.0	0.0	0.0	0.0
Organic matter (milligrams)	1.7	1.0	1.3	1.4
Ratio of organic matter in solution to dry matter in plant	1:37.0	1:65.3	1:50.5	1:38.1
Organic nitrogen in deposit (milligrams)	0.0	0.4	0.8	0.6
Nitrogen in organic matter in solution (per cent)	0.35	0.27	0.27	0.27

The plants used in this experiment made a rather rapid growth, the conditions in the greenhouse during May and June being very favorable for the growth of maize. Not only had all of the nitrate and ammonia nitrogen disappeared from the solution, but the organic nitrogen had been reduced to a very small quantity, being, in fact, lower than in any of the other experiments of this kind. It was rather surprising under the circumstances to find so much total organic matter in the solution. Evidently but a small proportion of the organic matter present was of a nitrogenous character, as the percentage of nitrogen in the organic matter in solution is only about 0.3. Probably there was much carbohydrate material present. Knudson's (1920) investigations led him to conclude that reducing sugars are excreted by plant roots. Calculating the nitrogenous organic matter at 6.25 times the nitrogen present, such material would constitute only about one-fifth of the total organic matter. It is altogether likely that the proportion of nitrogen in the organic matter varies at different stages in the growth of the plant.

The ratio of the organic matter in the solution to the dry matter in the plant is surprisingly high. This varied from one part in the solution to

37 parts in the plant, which was the narrowest ratio, to one part in the solution to 65.3 parts in the plant, which was the widest ratio. If it is to be assumed that the decomposition of this organic matter in the soil would increase its liberation by the plant, the result would be that a very large quantity of organic matter would be transferred to the soil. It is entirely conceivable that higher plants may influence bacterial activity in the soil by means of this liberation of organic matter, which would furnish a source of energy for certain bacteria, as, for instance, nitrate consumers.

In the solutions in which these four plants grew there were at harvest no ammonia, no nitrates, and very little organic nitrogen, which condition indicates a strong demand for nitrogen by the plants. Sometimes ammoniacal nitrogen was found to be present in the solutions and sometimes it was absent. The cause of its formation is an unsolved problem. Two possibilities present themselves. One is that ammonification of the organic matter in the solution took place between the time when the flask was opened and the time when the test for ammonia was made, contamination of the solution from outside occurring after the flask was opened. This was guarded against as far as possible. Another hypothesis is that ammonia formation was due to enzymic action, the plants having liberated the necessary enzymes.

Possibly ammonia is commonly formed and when the demand of the plants for nitrogen is great it is absorbed and thus disappears from the solution. If it is derived from the liberated organic nitrogen, as seems possible, it may be the means by which organic nitrogen is rendered available to higher plants.

In a previous experiment, flasks were opened at four different stages in the growth of maize. As the periods of growth varied from a rather early stage, before the nitrate nitrogen was all removed from the solution, to maturity, it would have been a very interesting experiment had it not been for the fact that the last two flasks opened were found to be contaminated. The data, however, are all tabulated in table 4, altho there is, of course, no assurance that the results were not materially affected by the organisms that had gained access to the solutions.

The sterile flasks in this experiment agree with those in the experiment recorded in table 3 in showing the presence of a large amount of organic matter in the solution in which the plants grew. The amount was less

for the data shown in table 4, but the growth of the maize plants in the sterile flasks also was less. The quantity of inorganic matter and of organic matter appears to decrease and increase at the same periods if credence is to be given to the data from the last two flasks opened. The

TABLE 4. TOTAL ORGANIC MATTER AND NITROGEN PRESENT IN SOLUTIONS AT SUCCESSIVE STAGES IN THE GROWTH OF MAIZE

Kind of plant	Maize	Maize	Maize	Maize
Serial no.	1	2	3	4
Date of setting plant in flask	June 28	June 28	June 28	June 28
Date of removing plant from flask	Aug. 3	Aug. 16	Aug. 30	Sept. 20
Growing period (days)	36	49	63	84
Dry matter in plant (milligrams)	10,200.0	24,100.0	32,200.0	65,000.0
Volume of solution at harvest (cubic centimeters)	6,200.0	6,950.0	2,850.0	2,790.0
Condition of solution	Sterile	Sterile	Contaminated	Molds
Nitrogen as nitrates in solution (milligrams)	32.4	Trace	0.0	0.0
Inorganic matter in solution (milligrams)	1,333.0	1,056.4	310.6	460.3
Organic matter in solution (milligrams)	291.4	284.9	76.9	251.1

data for inorganic matter were probably not influenced by the infection of flask no. 3, and this shows a gradual decrease in amount up to the sixty-third day of growth and then an increase at maturity, indicating a liberation of salts from the plant. Such liberation must, of course, have been by way of the roots. Admitting, then, that inorganic matter may be removed by the action of rainfall on the leaves, of which the investigations of Le Clerc and Breazeale leave little doubt, there appear to be at least two means by which this material may be liberated by the plant.

REDUCING AND OXIDIZING SUBSTANCES LIBERATED BY PLANT ROOTS

While many investigations have been made of the oxidizing and reducing enzymes in plants, very few have been undertaken for the purpose of ascertaining whether any of these bodies appear in the substratum in which the roots of plants are immersed. It was thought that the sterile solutions used in the experiments described above, in which plants of different kinds and of different stages of growth were produced, would permit of a series of tests for these substances under conditions that would exclude contamination from the seed or from outside sources,

and that these tests might possibly afford some information regarding the relation of the stage of growth of the plants to the presence of oxidizing or reducing substances.

REVIEW OF LITERATURE

Apparently the only examinations designed to detect the presence of reducing substances in media in which plants grew were those conducted by Schreiner and Sullivan (1910), who placed the roots, and in some cases the seeds also, of wheat seedlings in solutions of various reagents commonly used for detecting the presence of reducing substances. Considering only the tests in which roots alone were introduced into the reagent solution, these authors obtained reactions with starch-iodide solution, sodium selenite, and sodium tellurite. Tests for reduction of nitrates appear to have been made only where the seeds were present, and under these conditions nitrites were found by means of the Griess reaction. The seeds from which the seedlings were germinated had previously been treated with a 0.1-per-cent solution of mercuric chloride. The solutions in which the plants grew were not shown to be sterile.

It is well known that oxidizing enzymes occur within plant tissues and they are believed to play an important part in physiological processes. They have been found also in soils, but this does not furnish any proof that they are liberated by plant roots altho it suggests such a possibility. The presence in soils of large numbers of bacteria many of which are known to secrete enzymes, may well account for the appearance in soils of oxidizing enzymes without any contribution from roots of higher plants. It is equally true that the occurrence of enzymes within the plant would not necessarily lead to the conclusion that they are thus conveyed to the soil.

Not many investigators have taken up studies concerning the liberation of oxidizing substances by plant roots. The work of Molisch, Czapek, and Raciborski has been reviewed by Schreiner and Reed (1909), and hence it is not necessary to review it here. Schreiner and Reed, in the paper referred to, state that they have been able to detect the presence of oxidizing enzymes on certain parts of the surface of wheat roots. For this purpose they used alpha-naphthylamine, benzidine, vanillin, vanillic acid, phenolphthalin, aloin, and leuco-rosolic acid. As in their experiments for the detection of reducing substances, there was no evidence offered

to show that the solutions were sterile, but the authors state that it is improbable that the enzymes were produced by bacteria.

Summarizing the experiments to determine the presence of oxidizing enzymes outside of the growing roots of plants, it may be said that Molisch, Raciborski, and Schreiner and Reed report the finding of these enzymes and consider them to have been excreted by the roots as a normal condition of their growth. Evidence of the liberation of reducing substances is less conclusive, but if oxidizing enzymes are liberated by plant roots it is easily conceivable that reducing substances would be also, as both are well known to occur within the plant tissues.

TESTS FOR REDUCING AND OXIDIZING SUBSTANCES LIBERATED BY PLANT ROOTS

The data already presented show that a comparatively large amount of soluble organic matter may be given off by plant roots during the growing period. This organic matter may be derived in part from root caps and root hairs that are sloughed off by plant roots as development proceeds. The roots or detached cells may give up to the surrounding medium certain specific compounds, some of which may be enzymic in character. In order to obtain information on this subject a number of tests were made to detect the presence of certain substances that might influence reduction or oxidation.

Reducing substances

A number of reagents that had been proposed for the detection of the presence of reducing substances were used for testing the solutions in which maize plants had grown, and at the same time for testing check solutions consisting of the nutrient solution made up as it was for the growth of the maize plants. In some cases the solutions in which the plants had grown were boiled before being tested, but an unboiled portion was always tested at the same time. Some of the reagents failed to give a reaction with any of the solutions tested and were discarded. These were methylene blue, methyl violet, gentian violet, sodium selenite, and sodium tellurite. These failures may mean merely that the conditions under which their reactions occur did not obtain altho reducing substances may have been present.

Tests for reducing substances were made with prussian blue in solutions from six sterile flasks in which maize plants had grown, using both the unboiled and the boiled samples of the solutions as well as check nutrient solutions. These tests were made in solutions taken from plants at different stages of growth. Ten cubic centimeters of each solution was used, and each received two drops of a 0.5-per-cent solution of phenol. After the prussian blue was added, the tubes containing the solutions were allowed to stand for twenty-four hours, at the end of which time notes were taken on the results. In each of the six tests the unboiled solution in which the plant had grown gave a distinct reaction for reducing substances. The boiled solution gave no reaction in three tests, while in the other three the result was rather uncertain. The check solution gave no definite test for reducing substances.

Reduction of nitrates.— Since traces of ammonia were found in the sterile solution which had surrounded the maize roots, it was thought possible that thru the action of enzymes liberated by the plant this ammonia might have been formed from the nitrates in the nutrient solution. Tests for nitrates were made, using sulfanilic acid and naphthylamine acetate. No positive results were obtained. As a further test the diphenylamine reagent was employed. This reagent is considered to be positive to nitrite 1 part in 32,000,000 and to nitrate 1 part in 44,000,000. The tests were made with a series of sixteen flasks and no positive results were obtained.

This does not necessarily show, however, that reducing enzymes might not have been present, for the maize removed all the nitrates from the nutrient solution rather early in its development, and the liberation of reducing substances may not occur until after the plant has taken up most of the nutrients necessary for its development, or the nitrites may be absorbed by the plant.

The nitrites might not have been present because there were no nitrates from which they could be formed. The problem of supplying the nitrates and making the nitrite test was conducted as follows: Check flasks, twelve in number, were prepared with the same nutrient solution that was used for growing plants. A like number of test flasks were used which contained solution from around the plant roots. One hundred cubic centimeters was used in each flask, and the nitrate content was made equal in both check and test flasks. The flasks received phenol

to make the concentration 1 to 500, and were placed in the incubator at 23° C. The next morning tests were made for nitrites, using the Griess reagent. No visible differences were apparent. A second test for nitrites was made after forty-eight hours. The result was positive in every case. This test was repeated with the solution from another flask in which a maize plant had grown. While not so striking, the results in this case were also positive. Some tests were negative. A difference of NO_3 readings was not detectable in a colorimeter.

Another series of tests for nitrate reduction was conducted, using 5 cubic centimeters of the solutions in which maize plants had grown for periods of varying lengths and adding to this a small quantity of calcium nitrate solution, at the same time introducing two drops of a 0.5-per-cent solution of phenol. Alpha-napthylamine and sulfanilic acid were used to test for the presence of nitrites, the solutions being allowed to stand for certain lengths of time varying from two hours to three days. Such tests were made of the sterile solutions from eight flasks in which plants had been grown, the solutions being taken for the tests within a few minutes after the flasks were opened. A sample of the solution from each of the flasks except one was boiled before being tested, and another sample was not so treated. The check nutrient solution was tested in each case. Of the eight flasks tested, the unboiled solutions showed the presence of nitrites in every case but one, the check solution showed the absence of nitrites in six cases out of eight, and the boiled solution gave a reaction for nitrites in six tests but did not color so rapidly as did the unboiled. Apparently nitrate-reducing substances were usually present in the unboiled solutions in which the maize plants had grown, and boiling the solutions failed to render these substances incapable of bringing about reduction of nitrates in the presence of phenol.

While the process of boiling did not completely prevent the liquid surrounding the plant roots from effecting reduction of nitrates, it seemed to curtail its activity, as is indicated by the slower coloration of the reaction with the alpha-napthylamine and sulfanilic acid. The tests for reducing substances by means of prussian blue, on the other hand, did not give any more reaction with the boiled solutions than with the checks. While, therefore, the operation of boiling produced some effects corresponding to what might be expected from enzymes, there is some question as to

whether the reducing substances were of that nature in view of the results with reduction of nitrates.

Oxidizing substances

Peroxidases were detected in the culture solution in which the roots of maize, vetch, oats, peas, soybeans, alfalfa, and timothy had grown. From 8 to 10 cubic centimeters of each solution was placed in a dry test tube together with a few drops of hydrogen peroxide. This was allowed to stand for from two to three minutes, and then from two to three drops of a 5-per-cent phenol solution were added. The latter was then followed by an alcoholic solution of guaiac. It was considered that a positive test was recorded if the color became blue in thirty minutes. With this test no difficulty was experienced in obtaining a reaction with solutions from all of the flasks tested. Boiled solutions treated likewise gave no reactions.

In working with the solution in which vetch roots had grown, a very strong reaction was obtained by the use of hydrogen peroxide and phenol. The solution was placed in dry test tubes and a few drops of hydrogen peroxide were added. This was allowed to stand at room temperature. After from three to four minutes a few drops of a 5-per-cent phenol solution were run down the side of the test tube. Shortly after contact of the materials, a growing yellow color developed, which gradually increased and on long standing settled out. This test was negative when the same solution was boiled. An extract of macerated vetch roots and nodules gave the same test. If this material was boiled, however, no reaction was obtained.

Phenolpthalin was used as a reagent for indicating the presence of oxidizing substances in the solutions in which maize plants had grown. For these tests both boiled and unboiled samples of the solutions were used. Checks consisting of the nutrient solution in which no plants had grown were also included. Phenol was added, as in the previous tests. Results from these tests were usually negative.

Experiments in which guaiac were used without a peroxide indicated the presence of an oxidase in solutions in which maize plants had grown only when the plants were very young. Agar in which timothy plants were grown always gave a reaction with guaiac.

Tests with pyrogallol included only one sterile flask. No phenol was used. At the end of one-half hour the boiled solution was clear, the

unboiled was brown, and the check was a light yellow. On the whole the tests for oxidizing substances cannot be said to have offered very strong evidence of their presence except in the case of peroxidases.

Possible coexistence of oxidizing and reducing substances

Altho the number of tests for oxidizing enzymes were rather few, reactions indicating their presence were confined mainly to the solutions from flasks which gave no marked response to tests for reducing substances. It seems likely that both classes of substances are coexistent in solutions in which plants are growing, and that at one time the oxidizing substances may be dominant and at another the reducing substances. Differences in the intensities of the reactions at various times may thus be accounted for. Apparently with the maize plant the predominating reaction was for reducing substances thruout most of the stages of growth.

It would appear from these experiments that some form of reducing substance is always present in the solutions in which plants are growing. Whether oxidizing substances are always present, it is more difficult to say. They were found in some of the solutions taken from flasks in which the plants had reached only an early stage of growth, and unless they are destroyed later on they must be present thruout the entire life of the plant. In the natural soil solution, enzymes might be destroyed and thus removed from active operation except when freshly liberated.

Nature of oxidizing and reducing substances

Boiling the solutions in which plants had grown completely terminated the activities of the oxidases, as was to be expected. It did not always have that effect on the reducing substances, especially the nitrate reducers. There would thus seem to be considerable doubt as to whether the reducing substances were enzymic in character, but they at least had the power of bringing about reduction of nitrates in the absence of bacteria.

SUMMARY

Plants were grown with their roots in large flasks (8 or 12 liters capacity) containing a nutrient solution, the entire contents of the flasks being sterile. At various stages in the growth of the plants they were removed from the flasks and analyzed for nitrogen, and the nutrient solution was

tested for sterility and analyzed for nitrates, nitrites, ammonia, and organic nitrogen, and in some cases for total organic matter. A determination of organic nitrogen in the deposit at the bottom of the flasks was also made.

The plants grown were maize, oats, peas, and vetch. The nutrient solutions in which each of these plants grew contained nitrogen only in the form of nitrate when the plants were set in the flasks, but when the plants had grown for several weeks there was always organic nitrogen present. Even before the nitrate nitrogen had all been absorbed by the plants, organic nitrogen appeared in the solutions.

The deposit at the bottom of each flask contained a small quantity of organic nitrogen, which was probably derived from sloughing off of the root cells as indicated by the presence of plates of cells in the deposit. There was no direct evidence that the organic nitrogen in solution was liberated in any other way, but it is questionable whether such a large quantity could all come from these cells, especially during the early stages of growth.

A pea plant which grew in a solution without the addition of combined nitrogen liberated organic nitrogen into the solution in which it grew. The growth was by no means as vigorous as that of another pea plant which was furnished with nitrate nitrogen, and the plant itself contained only about one-fifth as much nitrogen as did the latter plant, but it liberated more than half as much organic nitrogen.

A series of flasks in which maize was growing were harvested at successive stages in the growth of that plant, and the plant and the flask contents were examined in the manner already described. Organic nitrogen appeared in the solutions at all stages in the growth of the plants, but there seemed to be a tendency for it to decrease in amount with progressive stages in the life of the plant and especially as the plant closely approached maturity. The organic nitrogen in the deposit at the bottom of the flasks did not show any decided tendency to vary in amount with the successive stages of plant growth.

Determinations of total organic matter were made in the solutions from some of the flasks. This constituent was very large in amount as compared with the nitrogenous organic matter present. Apparently there was much non-nitrogenous organic matter in the solutions. Calculating the nitrogenous organic matter at 6.25 times the nitrogen present,

this material would constitute only a small part of the total organic matter.

The presence of reducing substances in solutions in which plants had grown was indicated by certain tests, but a number of other reagents failed to give reactions. Nitrates were nearly always reduced in these solutions in the presence of an antiseptic. Boiling the solution did not entirely prevent nitrate reduction, but it greatly decreased the rate at which reduction proceeded.

Peroxidases were always present in solutions in which plants had grown. Boiling these solutions caused them to give no reaction for peroxidases. Tests for other oxidizing substances were not sufficiently satisfactory to warrant the conclusion that they were present.

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LYSIMETER EXPERIMENTS—II

RECORDS FOR TANKS 13 TO 16 DURING THE YEARS 1913 TO 1917 INCLUSIVE

T. LYTTLETON LYON AND JAMES A. BIZZELL

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CONTENTS

PAGE

The soil used 51
Volume weight 52
Mechanical composition 52
Chemical composition 53
Manure and fertilizers used 54
Methods for chemical and mechanical analyses 54
Soil treatment and cropping system 54
Quantity and rate of percolation 56
Percentage percolation of rainfall 56
Effect of liming on percolation 57
Water utilization by crops 58
Evapo-transpiration ratio 58
Moisture relations of crops 60
Removal of nitrogen from the soil in drainage water and in crops 61
Effect of liming on removal of nitrogen in crops 61
Effect of liming on removal of nitrogen in drainage water 62
Effect of liming on removal of nitrogen in both drainage water and crops 62
Relation of different crops to formation of nitrates 63
Removal of calcium 64
Effect of plant growth on removal of calcium 64
Effect of liming on removal of calcium 66
Liming to maintain the calcium content 67
Removal of magnesium 68
Effect of plant growth on removal of magnesium 68
Effect of liming on removal of magnesium 69
Removal of potassium 69
Effect of plant growth on removal of potassium 70
Effect of liming on removal of potassium 71
Removal of sulfur 72
Effect of plant growth on removal of sulfur 72
Effect of liming on removal of sulfur 73
Removal of phosphorus 73
Divergent effects of liming the two soils 74
Summary 76
Appendix (containing tables) 78
Tabular statement of crop yields from tanks 13 and 15, by years 78
Tabular statement of flow of drainage water from tanks 13 to 16, by months 78
Tabular statement of flow of drainage water by years 80
Tabular statement of meteorological records at Ithaca from May 1, 1913, to April 30, 1918 81
Tabular statement of substances contained in drainage water, in parts per million 83
Tabular statement of substances contained in drainage water, in pounds per acre 87
Tabular statement of ash and ash constituents in crops, in percentage of dry matter 92
Tabular statement of ash and ash constituents in crops, in pounds per acre 93

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T. Lyttleton Lyon and James A. Bizzell

The object of the experiments herein described was, in the main, similar to that of the lysimeter experiments previously reported by the authors,[1] the essential differences being that a soil of another series was used, and that the effect of different cropping systems on the removal of the soil constituents in the drainage water was not a feature of the present experiment. The lysimeter tanks were like those described in the earlier publication.

THE SOIL USED

The tanks were filled in the summer of 1910 with a soil classified by the United States Bureau of Soils as Volusia silt loam. The soil is typical of much of the hill land of southern New York. It was formed, in the main, from shale and sandstone as the result of glaciation, which was rather feeble on these high lands. There is much broken shale distributed thru the soil, the pieces varying in size from small particles to large rocks. The subsoil is often very compact, and even on the hillsides poor drainage is the rule. The soil layer is often shallow on the hills, the shale in some places lying three or four feet below the surface.

In chemical composition this soil is distinguished by its low content of calcium. The other soil constituents are present in what may be considered fairly liberal quantities. Agriculturally Volusia silt loam ranks as poor, and the sample placed in these lysimeter tanks is considerably less productive than the average soil of the type. It is a much less productive soil than the Dunkirk clay loam contained in tanks 1 to 12. Its low productivity as a type may be due in part to its location, which is mainly on high elevations, the approaches to which are steep, making it inaccessible to railroads and thus adding to the difficulty of applying lime and fertilizers, which have consequently been meagerly used on these lands.

[1] Lyon, T. Lyttleton, and Bizzell, James A. Lysimeter experiments. Records for tanks 1 to 12 during the years 1910 to 1914 inclusive. Cornell Univ. Agr. Exp. Sta. Memoir 12:11-15. 1918.

Acknowledgment.— The authors wish to express their thanks to Mr. E. W. Leland for his services in measuring and sampling the drainage water during the entire period of the experiments, and for supervising the cultural operations on the tanks.

Volume weight

Before the soil was placed in the tanks all stones larger than a walnut were removed from it, but, as is characteristic of this soil series, a large number of small stones still remained. It is probably on this account that the volume weight of the soil was so high. The weight of each twelve-inch layer of air-dry soil placed in the tanks is shown in table 1:

TABLE 1. AVERAGE WEIGHT OF EACH TWELVE-INCH LAYER OF SOIL IN TANKS

	First foot (pounds)	Second foot (pounds)	Third foot (pounds)	Fourth foot (pounds)
Weight of soil in tanks	2,250	2,170	1,850	1,750
Weight of soil per acre	5,625,000	5,425,000	4,625,000	4,375,000

This, it may be remarked, is a soil having greater volume weight than the Dunkirk clay loam used in tanks 1 to 12 inclusive, owing, in part at least, to the large number of stones.

Mechanical composition

A statement of the mechanical analysis of the soil by the centrifugal method, including all particles from fine gravel to clay, is given in table 2:

TABLE 2. MECHANICAL COMPOSITION OF SOIL IN FIELD FROM WHICH TANKS 13 TO 16 WERE FILLED

Separates	First foot (per cent)	Second foot (per cent)	Third foot (per cent)	Fourth foot (per cent)
Fine gravel	2.32	5.32	3.00	5.1
Coarse sand	2.91	4.83	2.78	5.2
Medium sand	3.02	4.64	2.85	5.1
Fine sand	6.32	8.60	6.30	9.1
Very fine sand	15.92	18.22	15.80	14.7
Silt	50.88	42.60	51.25	39.9
Clay	18.63	16.79	18.02	20.0

This soil has always permitted the rainfall to percolate readily since it has been in the tanks. At no time has there been any stoppage and there has never been any water standing on the surface. The soil has, on the whole, drained more quickly and given a clearer percolate than did the Dunkirk clay loam in tanks 1 to 12.

Chemical composition

The samples used for the mechanical analysis of the soil in these tanks were taken from each foot layer and represent the average composition of the four tanks. The samples for the chemical analysis were obtained in the same manner. Bulk analyses were made. The methods used are stated in the appendix to Memoir 12 (pages 85 to 87) and the results are given in table 3:

TABLE 3. CHEMICAL ANALYSIS OF SOIL PLACED IN TANKS 13 TO 16

Constituents determined	First foot	Second foot	Third foot	Fourth foot
Nitrogen (per cent)	0.145	0.052	0.059	0.050
Organic carbon (per cent)	1.560	0.270	0.115	0.080
Calcium oxide (per cent)	0.230	0.165	0.260	0.365
Magnesium oxide (per cent)	0.560	0.390	0.290	0.460
Potassium oxide (per cent)	1.690	1.810	1.710	2.170
Sodium oxide (per cent)	1.120	0.940	0.810	1.070
Phosphoric anhydride (per cent)	0.071	0.039	0.018	0.071
Sulfur trioxide (per cent)	0.042	0.033	0.041	0.031
Carbon dioxide as carbonate (per cent)	0.030	0.030	0.020	Trace
Lime requirement (CaO in parts per million)	1,350	800	650	400

The chemical analysis shows a relatively good supply of plant nutrients as compared with the average soil or with the Dunkirk soil in tanks 1 to 12, but the Dunkirk is a much more productive soil, as is evident on comparison of the yields of crops from both sets of tanks. The only elements in which the surface foot of the Volusia soil is materially below that of the Dunkirk are calcium and sulfur. Nitrogen, phosphorus, and potassium are about equal in amount in the two surface soils. The lime requirement according to the Veitch method is somewhat greater in the Volusia soil. In the second, third, and fourth feet the calcium is

much higher in the Dunkirk soil. If the difference in productiveness and other properties is to be traced to any difference in chemical composition, it would appear that calcium and possibly sulfur are the only constituents that would call for inspection. It is true, however, that magnesium is higher in the surface foot of the Volusia soil.

MANURE AND FERTILIZERS USED

Farm manure was applied once to the soil in each of the four tanks. This application was made in the spring of 1914. The analysis of the manure is given in table 4. The method of analysis is described in the appendix to Memoir 12, pages 90 and 91.

TABLE 4. COMPOSITION OF FARM MANURE APPLIED TO THE SOIL IN TANKS 13 TO 16

Constituents	Percentage composition	Pounds per acre
Dry matter	21.26	4,252
Nitrogen	0.50	100
Phosphoric anhydride	0.37	74
Potassium oxide	0.36	72
Calcium oxide	0.63	126
Magnesium oxide	0.27	54

The burnt lime, of which one application was made, contained 91.95 per cent of CaO and a trace only of MgO.

METHODS FOR CHEMICAL AND MECHANICAL ANALYSES

The methods used for the chemical analyses of the soil, crops, drainage water, rain water, manure, lime, and potassium sulfate, and for the mechanical analysis of the soil, are described in the appendix to Memoir 12, pages 85 to 91, inclusive.

SOIL TREATMENT AND CROPPING SYSTEM

The four tanks used in this experiment were all filled in the late summer of 1910. From that time until the spring of 1913 they were not treated in any way, but the drainage was collected, measured, and analyzed in

order to have a complete record of all constituents removed in the drainage water from the time when the soil samples were taken for analysis. Since the present report does not attempt to show the difference in the composition of the soil at a later period, but is rather a discussion of the effect of the application of burnt lime on the composition of the drainage water and the plant ash, the drainage for the period previous to May 1, 1913, is not considered.

Farm manure was applied to each of the four tanks in the spring of 1913, the application being at the rate of 10 tons to the acre. Burnt lime was applied to tanks 15 and 16 in the spring of 1913 at the rate of 3000 pounds to the acre.

Tanks 14 and 16 were never planted to any crop, and growth of vegetation on them was prevented by hoeing. In the year 1915, when maize was growing on tanks 13 and 15, the unplanted tanks were hoed at the same time and in the same way as were the tanks planted to maize; when other crops were growing on the planted tanks, the unplanted ones were merely scraped with a hoe. In each tank planted to maize there were eighteen maize plants. Seven rows of oats and the same number of rows of barley were sown in each tank planted to those crops. The barley was used to replace wheat, which had been sown in the previous autumn and had winterkilled. Canada peas were planted broadcast. All crops grew to maturity and produced seed, but it was evident that the soil was not a very productive one. The manure, lime, and crop treatments are shown in table 5:

TABLE 5. SOIL TREATMENT AND CROPS RAISED ON LYSIMETER TANKS 13 TO 16 DURING THE PERIOD FROM 1913 TO 1917

Tank	Soil treatment		Crops raised				
	Fertilizer	Lime	1913	1914	1915	1916	1917
13	Farm manure	None	Oats	Canada peas	Maize	Oats	Barley
14	Farm manure	None	None	None	None	None	None
15	Farm manure	Burnt lime	Oats	Canada peas	Maize	Oats	Barley
16	Farm manure	Burnt lime	None	None	None	None	None

QUANTITY AND RATE OF PERCOLATION

The rainfall that percolated thru the soil was measured by monthly periods, and a record of each tank by months is therefore available. It is thus possible to ascertain the effect of certain treatments, such as lining and cropping, on the proportion of the rainfall passing thru the soil, and even to compare the relative permeability of the two soils.

Percentage percolation of rainfall

The figures for the flow of drainage water from each of the lysimeter tanks 13 to 16, expressed in liters for each month from May 1, 1913, to April 30, 1918, are given in table 2 of the appendix (pages 78 to 80). The flow calculated to acre inches annually for the same period is given in table 3 of the appendix (page 80). These tables furnish the data from which the average annual percolation in inches from the unplanted soil may be found, and also that from the soil on which crops grew. This, together with the percentage percolation, is given in table 6. The rainfall during the five-years period averaged 32.97 inches annually.

TABLE 6. AVERAGE ANNUAL PERCOLATION OF RAINFALL FROM UNPLANTED AND FROM PLANTED SOIL DURING FIVE-YEARS PERIOD

Tanks	Crop treatment	Average annual percolation	
		Inches	Per cent of rainfall
14, 16	No plants allowed to grow	27.13	82.3
13, 15	Plants raised every year	20.62	62.5
	Difference in percolation	6.51	19.8

On the basis of these figures, about four-fifths of the rainfall percolated thru the bare soil and three-fifths thru the cropped soil. Somewhat more than one-fifth of the rainfall may therefore be considered as being used by the crops, since the evaporation from the surface of the unplanted soil may be assumed to be greater than that from the surface of the planted soil. This, however, is only a small proportion of the total rainfall and would account for only about six and one-half to seven inches of the annual precipitation.

Comparing the figures for percolation thru the Volusia soil with those thru the Dunkirk, given in the earlier publication already referred to, it will be seen that the former soil is more permeable than the latter and that the crops on the former used about an inch more rainfall.

In table 4 of the appendix (pages 81 to 83) are given the weather records at Ithaca by months, including the rainfall, the mean maximum, mean minimum, and mean temperatures, the hours of sunshine, the average hourly velocity of the wind, and the mean humidity of the air, for the period from May 1, 1913, to April 30, 1918.[2] These data were obtained at a distance of somewhat less than a mile from the lysimeters.

Effect of liming on percolation

As already stated, tanks 15 and 16 received an application of burnt lime at the rate of 3000 pounds to the acre. It has frequently been said that liming, especially with burnt lime, has a tendency to make a heavy soil more permeable to water. If such has been the effect of the lime on this soil, it may possibly be shown by comparing the volume of drainage water from the limed and the unlimed tanks. There may be some question, however, whether any flocculating action which the lime may have had on the upper six or seven inches of soil with which it was incorporated would increase the amount of percolation thru the entire four feet of soil. Comparisons would best be made between limed and unlimed tanks that have otherwise received similar treatment, and this is done in table 7. It is evident from this table that the application of lime has

TABLE 7. AVERAGE ANNUAL PERCOLATION OF RAINFALL THRU LIMED AND UNLIMED SOIL DURING FIVE-YEARS PERIOD

Crop treatment	Fertilization	Soil not limed		Soil limed	
		Tank	Flow (acre inches)	Tank	Flow (acre inches)
No plants allowed to grow.....	Farm manure.	14	28.60	16	25.66
Oats, peas, corn, oats, barley...	Farm manure.	13	21.28	15	19.96
Average.....			24.94		22.81

[2] The authors are indebted to Dr. W. M. Wilson for the weather records at Ithaca.

not caused a greater percolation of water. The same was true of the application of lime to the Dunkirk soil in tanks 1 to 12, in the earlier experiments. While this may not mean that the lime did not flocculate the upper layer of soil with which it was incorporated, it has some significance so far as drainage is concerned, since it indicates that liming a soil of this kind would not result in facilitating the removal of water thru tile drains.

WATER UTILIZATION BY CROPS

The water utilization by crops on this soil was large for the amount of dry matter produced, both when calculated to the minimum transpiration ratio and by the evapo-transpiration ratio. The former was calculated by subtracting the drainage from the planted tanks from the drainage from the unplanted ones, and amounts to 451 pounds of water for every pound of dry matter in the crops raised during the five-years period. This appears in tabular form in table 8:

TABLE 8. Minimum Transpiration for All Crops Raised during Five-Years Period

Tanks	Cropping treatment	Average annual percolation per tank (pounds)	Average annual production of dry matter per tank (pounds)
14, 16	Unplanted	2,462	.....
13, 15	Cropped	1,871	1.31
Minimum transpiration		591	.....
Minimum transpiration ratio		1:451	.....

Evapo-transpiration ratio

The evapo-transpiration ratio was calculated by subtracting the average percolation thru the planted tanks for the five-years period from the rainfall on the same area for the same period, and dividing this by the number of grams of dry matter per tank in the crops produced. This ratio is given in table 9:

TABLE 9. EVAPO-TRANSPIRATION FOR ALL CROPS RAISED DURING FIVE-YEARS PERIOD

	Liters per tank
Rainfall (average annual)	1,388.7
Percolation from planted tanks (average annual)	848.7
Transpiration and evaporation from planted tanks	540.0
Evapo-transpiration ratio	1:908

Neither the minimum transpiration ratio nor the evapo-transpiration ratio is necessarily the same as the actual transpiration ratio. The former is likely to be less because the evaporation from the unplanted soil is almost always greater than the evaporation from the planted soil, and the latter is almost sure to be greater because it includes the water that evaporates from the surface of the soil as well as that which is transpired by the plants. The actual transpiration ratio therefore lies between 1:451 and 1:908.

It is significant that both transpiration ratios for the Volusia soil are so much wider than those for the Dunkirk soil, the former being about 56 per cent wider than the latter in both cases. It seems fair to assume that the actual transpiration ratio is correspondingly wider for the Volusia soil. Such differences cannot be attributed to conditions other than the soil, and probably arise from a difference in the concentration of the soil solution. The transpiration ratios are inversely proportional to the concentration of the drainage water and the crop yields from these two soils, as may be seen in table 10, the data in which are for the five-years periods already reported with the exception of the crop yields, which are for 1915, 1916, and 1917 only, since those were the only years in which the same crops were grown on both sets of tanks.

TABLE 10. RELATION OF TRANSPIRATION RATIOS, TOTAL SOLIDS IN DRAINAGE WATER, AND CROP YIELDS

	Minimum transpiration ratio	Evapo-transpiration ratio	Total solids in drainage of unplanted tanks (parts per million)	Crop yields in 1915–1917 (grams per tank)
Volusia silt loam	1:451	1:908	297.7	3,359.0
Dunkirk clay loam	1:290	1:580	401.5	6,478.3

It would appear from the data presented in table 10 that an economic utilization of water by the plant accompanies a high concentration of the water passing thru the soil, and that there is, moreover, a relation between the concentration of this water and the productive ability of the soil.

Moisture relations of crops

In table 11 is given a statement of the moisture relation of each crop grown on these tanks during the five years of the experiment. The

TABLE 11. MOISTURE RELATIONS OF CROPS ON TANKS 13 AND 15 DURING THE PERIOD FROM 1913 TO 1917

Year	Tanks	Crop	Minimum transpiration ratio	Evapo-transpiration ratio	Transpiration and evaporation (acre inches)	Dry matter in crops (pounds per acre)	Rainfall in percolate (per cent)
1913	13, 15	Oats	1:373	1:690	10.13	3,542	65.08
1914	13, 15	Canada peas	1:525	1:1005	14.08	3,316	54.31
1915	13, 15	Maize	1:332	1:613	12.68	4,977	64.49
1916	13, 15	Oats	1:366	1:1108	11.85	2,546	54.75
1917	13, 15	Barley	1:755	1:1618	13.06	1,858	69.80

minimum transpiration ratios for all these plants are higher than for the same plants grown on the Dunkirk soil, and the evapo-transpiration ratios also are higher. These discrepancies emphasize the futility of trying to determine a standard for the water requirements of plants when soil is used as the medium in which the plants are grown.

REMOVAL OF NITROGEN FROM THE SOIL IN DRAINAGE WATER AND IN CROPS

There are large differences between the planted and the unplanted tanks in respect to the nitrogen removed in the drainage water, the amount from the unplanted tanks being in all cases larger. Nitrogen in the drainage water was all in the form of nitrates. There are considerable differences in the quantities of nitrogen removed from any one tank from year to year. In the unplanted tanks these differences do not appear to be associated with any weather conditions shown in the monthly records. It is possible that conditions extending over shorter periods may have influenced the production of nitrates. In the case of the tanks filled with Dunkirk soil in the earlier experiments, the removal of nitrogen appeared to be influenced by the total yearly rainfall for the year beginning May 1, but this does not account so satisfactorily for the removal of nitrogen from the Volusia tanks. Future experiments may throw more light on these relations.

Effect of liming on removal of nitrogen in crops

One of the beneficial effects which lime frequently exerts on soil showing a lime requirement is to promote the formation of nitrates from organic nitrogenous compounds. Such action might be reflected in the nitrogen content of the drainage water or in the nitrogen removed in the crops.

The amount of nitrogen removed in the crops produced each year of the experiment is shown in table 12:

TABLE 12. NITROGEN IN CROPS, CALCULATED TO POUNDS PER ACRE BY YEARLY PERIODS

Tank	Burnt lime (pounds)	Nitrogen in crops (pounds per acre)					
		Oats 1913	Peas 1914	Maize 1915	Oats 1916	Barley 1917	Total
13	None	34.98	68.75	28.35	21.74	18.79	172.61
15	3,000	36.24	94.86	37.41	24.93	23.74	217.18

It is apparent from the data presented in table 12 that in every year the crops on the limed soil contained more nitrogen than did the crops on the soil that was not limed. This, of course, is not positive proof that lime increases the production of nitrates in this soil, as nitrogen may not be

an important factor in crop production; on the other hand, it may be significant, especially if it is supported by evidence drawn from the removal of nitrogen in the drainage water.

Effect of liming on removal of nitrogen in drainage water

The quantities of nitrate nitrogen removed in the drainage water of unplanted soil afford a better means of ascertaining whether liming increases nitrate formation than does the removal of nitrogen in crops. The data by years for the nitrogen in drainage water from unplanted soil are presented in table 13:

TABLE 13. NITROGEN IN DRAINAGE WATER OF UNPLANTED TANKS, CALCULATED TO POUNDS PER ACRE BY YEARLY PERIODS (MAY 1 TO APRIL 30)

Tank	Fertilizer	Burnt lime (pounds)	Nitrogen in drainage water (pounds per acre)					
			1913	1914	1915	1916	1917	Total
14.....	Manure..	None	73.41	34.21	49.31	34.47	38.71	230.11
16.....	Manure..	3,000	88.45	49.56	55.79	50.80	46.19	290.79

In each year the removal of nitrogen in the drainage water from the limed soil was greater than from the unlimed, which is very good evidence that the lime produced a condition more favorable to the production of nitrates. It may be remarked that the application of lime to the Dunkirk soil was not attended by any increase in the removal of nitrogen by the drainage water or by the crops. This difference in effect of lime is all the more striking inasmuch as the lime requirement of the surface foot of the Dunkirk soil is very little less than that of the Volusia. The percentage of calcium, however, is about one-third less in the surface foot of the Volusia. In this case the relative calcium content of the soil is a better guide to its need of lime for nitrification than is the lime requirement as determined by the Veitch method.

Effect of liming on removal of nitrogen in both drainage water and crops

While the nitrogen in the crops alone may not be an adequate guide to the effect of lime on the soil, the nitrogen in the crops added to that in the drainage water from the same tanks is perhaps somewhat more com-

prehensive. These data are given in table 14. It is apparent from this table that the application of lime to this soil results in an increased

TABLE 14. NITROGEN IN BOTH DRAINAGE WATER AND CROPS, CALCULATED TO POUNDS PER ACRE IN YEARLY PERIODS

Tank	Burnt lime (pounds)	Nitrogen in both drainage water and crops (pounds per acre)					
		Oats 1913	Peas 1914	Maize 1915	Oats 1916	Barley 1917	Total
13	None	46.03	74.47	44.78	26.96	23.51	215.75
15	3,000	57.46	114.16	51.67	28.81	28.10	280.20

removal of nitrogen in the combined crop and drainage water. There would seem to be little doubt, in view of the data presented in the last three tables, that the effect of lime on this soil is to increase nitrate formation.

RELATION OF DIFFERENT CROPS TO FORMATION OF NITRATES

It has been noted that the experiments with Dunkirk soil indicated certain rather definite relationships between certain kinds of plants and the formation of nitrates. A similar relationship appears to exist in the experiments with Volusia soil, as may be seen in the data given in table 15:

TABLE 15. AVAILABLE NITROGEN IN SOIL PRODUCING DIFFERENT CROPS, AS MEASURED BY THE NITROGEN OF THE CROP AND OF THE DRAINAGE WATER

(In pounds per acre)

Crop	Nitrogen in planted tanks (average of tanks 13 and 15)				Nitrogen in drainage water in bare tanks (average of tanks 14 and 16)	Excess (+) or deficiency (—) in planted tanks
	In drainage water	In tops	In roots*	Total		
Oats (1913)	16	35	12	63	81	—18
Peas (1914)	12	81	27	120	42	+78
Maize (1915)	15	32	11	58	52	+ 6
Oats (1916)	4	23	8	35	42	— 7
Barley (1917)	4	21	7	32	42	—10

* Estimated at one-third the quantity in tops.

Estimating the nitrogen in the roots of each crop to amount to one-third the quantity in the above-ground part, it will be seen that the nitrogen in the oat crop added to the nitrogen in the drainage water from the tanks on which that crop grew was less in amount than the nitrogen in the drainage water from the bare tanks for the same period. The same was true of barley, but it was not true of maize or of peas. The excess of nitrogen from the pea tanks can doubtless be ascribed to the nitrogen-fixing properties of *Bacillus radicicola* in the nodules of the pea roots. The excess nitrogen from the maize tanks must be ascribed to some different phenomenon. It has been suggested[3] that some plants have the property of depressing the formation of nitrates, and that certain plants possess this property to a greater degree than do others. The data here presented are in line with such an hypothesis.

REMOVAL OF CALCIUM

Calcium was removed in the drainage water to a much greater extent than was any other of the bases determined, but in relatively small amounts by the plants. A comparison of the calcium in the drainage water of the Dunkirk and Volusia soils shows that the latter lost more calcium by leaching than did the former, in spite of the fact that this soil contained only about two-thirds as much of that element as did the Dunkirk soil. On the other hand, the crops grown on the Volusia soil contained less calcium but the yield of crops was much smaller. The total removal of calcium from the Volusia soil, from both planted and unplanted tanks, was greater than that from the Dunkirk.

Effect of plant growth on removal of calcium

In the experiments with Dunkirk soil it was found that less calcium was removed from the planted soil in crop and drainage water combined than was found in the drainage alone from the unplanted soil. This is true also of the Volusia soil, as may be seen from table 16:

[3] Lyon, T. Lyttleton, and Bizzell, James A. Some relations of certain higher plants to the formation of nitrates in soils. Cornell Univ. Agr. Exp. Sta. Memoir 1:1–111. 1913.

TABLE 16. AVERAGE ANNUAL REMOVAL OF CALCIUM FROM PLANTED AND FROM UNPLANTED TANKS

(In pounds per acre)

Tanks	Soil treatment	Calcium removed in		Total calcium removed
		Drainage water	Crops	
13, 15	Planted	256.4	8.7	265.1
14, 16	Bare	351.4	.....	351.4
Calcium conserved by cropping				86.3

The process of cropping conserves the calcium in the soil even when the entire crop is removed. The reason for the greater removal of calcium from the uncropped soil may be found, in part at least, in the large formation and leaching of nitrates when plants are not present. In table 17 are shown the average quantities of nitrates found annually in the drainage water of the planted and the unplanted tanks.

TABLE 17. AVERAGE ANNUAL REMOVAL OF NITRATES IN DRAINAGE WATER FROM PLANTED AND FROM UNPLANTED TANKS

Tanks	Soil treatment	Nitrates removed (pounds per acre)
13, 15	Planted	47.0
14, 16	Bare	231.7

The nitrates in the drainage water from the cropped soil would account for only about 11.5 pounds of calcium, while the nitrates from the unplanted soil correspond to about 56.5 pounds of calcium which might be removed in the form of nitrate. This would still leave about 245 pounds of calcium that had been removed in the drainage water from the planted soil in some form other than nitrate, and about 285 pounds from the unplanted soil.

The concentration of calcium in the drainage water from the planted and from the unplanted soil shows little difference, but this is in the same order as its total removal. This may be seen in table 18, in which is stated in parts per million the average calcium content for the five-years period.

TABLE 18. Average Calcium Content of Drainage Water from Planted and from Unplanted Tanks

Tank	Soil treatment		Calcium (parts per million)	
	Crop	Lime	For each tank	Average for crop treatment
13	Planted	Not limed	52.3	54.4
15	Planted	Limed	56.6	
14	Bare	Not limed	49.9	58.9
16	Bare	Limed	68.0	

The greater loss of calcium from the unplanted soil was not due entirely to the greater percolation of water thru that soil, since in that case the concentration would not be greater. It would appear that the presence of a large amount of a strong acid, such as nitric acid, in the unplanted soil would explain the greater concentration of the calcium in the drainage water of that soil as compared with the weaker carbonic acid in the planted soil.

Effect of liming on removal of calcium

The application of burnt lime to the Dunkirk soil at the rate of 3000 pounds to the acre in the earlier experiments did not result in increasing the quantity of calcium in the drainage water or in the ash of the crops produced. A similar application to the Volusia soil in this experiment appears to have decreased the amount removed in both of these ways, as may be judged from the data presented in table 19:

TABLE 19. CALCIUM IN DRAINAGE WATER AND IN CROPS
(In pounds per acre, annual average)

Tank	Burnt lime (pounds)	Calcium in drainage water	Calcium in crops	Total calcium
13	None	257.6	7.46	265.1
14	None	319.4	.....	319.4
15	3,000	255.1	10.09	265.2
16	3,000	383.4	.....	383.4

The figures for average annual calcium removal for the entire five-years period, as given in table 19, show a very large increase in the quantity of calcium leached out of the bare limed soil as compared with that from the bare soil unlimed; they show also a moderate increase in the calcium contained in the crops, but they do not indicate any effect from the liming on the calcium leached from the cropped soil. The evidence, however, is in favor of the conclusion that liming increases the amount of soluble calcium in Volusia soil, while it has no such effect on Dunkirk soil. This is hardly to be accounted for by the absorbent properties of the soil for lime, since Volusia soil has a somewhat higher lime requirement than Dunkirk as determined by the Veitch method.

The concentration of calcium was appreciably greater in the drainage from the limed soil than in that from the unlimed soil, both when planted and when kept free of vegetation, as may be seen in table 18.

Liming to maintain the calcium content

The Volusia soil, altho low in calcium, is annually losing a large quantity in the drainage water, particularly from the unplanted soil. The removal of calcium in the ash of crops has been small as compared with that in the drainage water. If the loss of calcium from the limed soil were to be replaced, it would require an annual application of 536 pounds of pure burnt lime, or 957 pounds of pure limestone, to supply the uncropped soil, and 371 pounds of burnt lime, or 662 pounds of limestone, to supply the planted soil with calcium to the amount removed in the crops and in the drainage water.

REMOVAL OF MAGNESIUM

Magnesium was removed in much smaller quantity than was calcium, both in the drainage water and in the crops. In both ways the removal was less from the Volusia soil than from the Dunkirk, altho the removal of calcium was greater.

Effect of plant growth on removal of magnesium

The effect of plant growth on the removal of magnesium is brought out by table 20. It will be seen that there is a greater loss of magnesium in

TABLE 20. AVERAGE ANNUAL REMOVAL OF MAGNESIUM FROM PLANTED AND FROM UNPLANTED TANKS

(In pounds per acre)

Tanks	Soil treatment	Magnesium removed in		Total magnesium removed
		Drainage water	Crops	
13, 15	Planted	30.6	3.5	34.1
14, 16	Bare	45.4	.....	45.4
Magnesium conserved by cropping				11.3

the drainage water of the uncropped soil than in both the drainage and the crops of the planted soil. The large quantity of magnesium leached from the bare soil is apparently caused mainly by the solvent action of the nitric acid, as was the case with calcium.

Not only is the total removal of magnesium greater from the bare than from the planted soil, but its concentration is greater in the water from the uncropped soil, as may be seen from table 21:

TABLE 21. AVERAGE MAGNESIUM CONTENT OF DRAINAGE WATER FROM PLANTED AND FROM UNPLANTED TANKS

Tank	Soil treatment		Magnesium (parts per million)	
	Crop	Lime	For each tank	Average for crop treatment
13	Planted	Not limed	6.1	6.3
15	Planted	Limed	6.6	
14	Bare	Not limed	7.3	8.2
16	Bare	Limed	9.2	

Effect of liming on removal of magnesium

The effect of liming the soil was to increase the removal of magnesium both in the leachings and in the crops, as may be seen in table 22. There

TABLE 22. AVERAGE ANNUAL REMOVAL OF MAGNESIUM FROM LIMED AND FROM UNLIMED TANKS

(In pounds per acre)

Soil treatment	Tank	Magnesium removed from planted tanks			Tank	Magnesium leached from corresponding unplanted tanks
		In drainage water	In crops	Total		
Not limed	13	29.6	3.06	32.66	14	39.30
Limed	15	31.7	3.93	35.63	16	51.60

appears to be a basic exchange, similar to that which occurred in the Dunkirk soil, by which magnesium was liberated and dissolved by the soil water. The concentration of magnesium also was greater in the drainage water from the limed soil than in that from the unlimed, as may be seen in table 21.

REMOVAL OF POTASSIUM

Potassium differs from the other bases that were determined in the Dunkirk soil in that it was removed in greater quantities by the crops than by the drainage water. This was not true of the removal of potassium from the Volusia soil.

Effect of plant growth on removal of potassium

In spite of the fact that less potassium was removed by crops than by drainage water in these experiments, the total removal of potassium was greater from the planted than from the bare tanks. This is entirely contrary to the removal of calcium from the same tanks, as may be seen in table 23:

TABLE 23. AVERAGE ANNUAL REMOVAL OF POTASSIUM FROM PLANTED AND FROM UNPLANTED TANKS

(In pounds per acre)

Tanks	Soil treatment	Potassium removed in		Total potassium removed
		Drainage water	Crops	
13, 15	Planted	73.2	34.1	107.3
14, 16	Bare	84.5	.....	84.5
Potassium conserved by not cropping				22.8

While the growth of crops conserved the calcium in the soil, the same operation increased the loss of potassium. There was little difference in the concentration of potassium in the drainage water from the planted and from the bare tanks, as is shown in table 24:

TABLE 24. AVERAGE POTASSIUM CONTENT OF DRAINAGE WATER FROM PLANTED AND FROM UNPLANTED TANKS

Tank	Soil treatment		Potassium in drainage water (parts per million)	
	Crop	Lime	For each tank	Average for crop treatment
13	Planted	Not limed	18.3	15.9
15	Planted	Limed	13.6	
14	Bare	Not limed	15.5	14.0
16	Bare	Limed	12.5	

In respect to the concentration of potassium in the drainage water from the bare and from the planted tanks, the Volusia and the Dunkirk soils are in accord. It is probable that this is to be accounted for, in part at least, by the greater volume of percolate from the bare soil, but it seems possible that the plant growth effects a solvent action on the soil potassium which is indicated by the fact that the total removal of potassium in the crops and in the drainage combined is greater than that in the drainage from the bare soil.

Effect of liming on removal of potassium

The application of lime to this soil resulted in a decrease in the quantities of potassium contained in the drainage water and in the crops. This is shown in table 25:

TABLE 25. AVERAGE ANNUAL REMOVAL OF POTASSIUM FROM LIMED AND FROM UNLIMED TANKS

(In pounds per acre)

Soil treatment	Tank	Potassium removed from planted tanks			Tank	Potassium leached from corresponding unplanted tanks
		In drainage water	In crops	Total		
Not limed	13	88.6	35.08	123.68	14	99.1
Limed	15	57.8	33.12	90.92	16	69.9

There is nothing in this experiment to indicate that the application of lime caused the liberation of potassium. The same was true of the experiment with Dunkirk soil. It may be remarked, however, that if the application of lime did liberate any potassium from the surface soil, it may have been absorbed by the lower layers of soil and thus have been removed from the drainage water.

The concentration of the drainage water from the limed and from the unlimed soil does not give any more indication of the liberation of potassium than do the quantities removed. The concentration of potassium is stated in table 26:

TABLE 26. POTASSIUM CONTENT OF DRAINAGE WATER FROM LIMED AND FROM UNLIMED TANKS

Tank	Soil treatment		Potassium (parts per million)
	Crop	Lime	
13	Planted	Not limed	18.3
15	Planted	Limed	13.6
14	Bare	Not limed	15.5
16	Bare	Limed	12.5

REMOVAL OF SULFUR

Sulfur was recovered in the drainage water as sulfate, and it is significant that the years in which the content of sulfur in the drainage water was large were the years in which the removal of nitrogen by leaching was large. Drainage water from the Volusia soil contained somewhat less sulfur than did that from the Dunkirk, but the crops on the former soil contained as much sulfur as did those on the latter altho the yields were much smaller.

Effect of plant growth on removal of sulfur

There is one respect in which nitrogen and sulfur differ radically in this experiment, and that is in the proportion removed by crops and by drainage water, respectively. Nitrogen is removed most largely by the crops on planted soil, while sulfur is carried off mainly by the drainage water. The figures for sulfur in crops and in drainage water during the period of the experiment are given in table 27. The total quantity of

TABLE 27. SULFUR IN DRAINAGE WATER AND IN CROPS
(In pounds per acre, annual average)

Tank	Lime treatment	Sulfur in drainage water	Sulfur in crops	Total sulfur
13	Not limed	35.2	9.6	44.8
14	Not limed	43.3	.....	43.3
15	Limed	33.7	10.7	44.4
16	Limed	39.0	.....	39.0

sulfur removed from the planted tanks is not materially different from that removed from the bare tanks.

Effect of liming on removal of sulfur

In the experiments with Dunkirk soil the application of lime was accompanied by an increase in the quantity of sulfur in the drainage water. In the present experiments this was not the case, as may be seen in table 28:

TABLE 28. AVERAGE ANNUAL REMOVAL OF SULFUR FROM LIMED AND FROM UNLIMED TANKS

(In pounds per acre)

Soil treatment	Tank	Sulfur removed from planted tanks			Tank	Sulfur leached from corresponding unplanted tanks
		In drainage water	In crops	Total		
Not limed	13	35.2	9.6	44.8	14	43.3
Limed	15	33.7	10.7	44.4	16	39.0

Liming the Dunkirk soil did not result in an increased formation of nitrates but apparently favored sulfofication. Application of lime to the Volusia soil was accompanied by increased nitrification but had no effect on the production of sulfates. This would perhaps indicate that the conditions favorable to one of these fermentations are not always favorable to the other.

REMOVAL OF PHOSPHORUS

The Volusia soil, like the Dunkirk, has never furnished more than a trace of phosphorus in the drainage water. The data on removal of this element are therefore confined to the ash analyses of the crops. The average annual removal of phosphorus (calculated to the element P) is shown in table 29:

TABLE 29. Phosphorus in Crops
(In pounds per acre, annual average)

Tank	Soil treatment	Phosphorus in crops
13	Not limed	9.36
15	Limed	11.12

There is a larger annual removal of phosphorus in the crops grown on the limed soil than in those from the unlimed soil. This was borne out by the data for each year, which are given in table 7 of the appendix (page 92). The year 1913 was the only one in which more phosphorus did not appear in the limed crops. In this respect there was no similarity between the Volusia and the Dunkirk soil, the latter having shown no increase in the quantity of phosphorus in the crops grown on the limed soil.

DIVERGENT EFFECTS OF LIMING THE TWO SOILS

Comparison of the results of applications of lime to the Dunkirk soil with those obtained from the Volusia soil shows some striking differences. It will be remembered that the Dunkirk soil contained about 50 per cent more calcium in the surface foot than does the Volusia soil, and that this ratio gradually increased with the depth, the fourth foot of the Dunkirk soil containing 319 per cent more than the corresponding layer of the Volusia. The lime requirement of the two soils by the Veitch method was about the same when averaged for the four feet, altho it was slightly greater in the surface foot of the Volusia. It is evident that the lime requirement as determined is not a measure of the calcium content of these soils.

In the light of this information it is interesting to observe the effect of liming in order to ascertain whether the calcium content or the lime requirement is the better guide to the need of the soils for lime as expressed by their response in crop yield. The records for the Dunkirk soil show that there was no larger yield on the limed tanks than on the unlimed. On the Volusia soil there was a consistently larger yield on the limed soil each

year except the first, and this increase averaged somewhat more than 12 per cent for the five-years period. The calcium content therefore appears to be a better guide to the need of these soils for lime than does the lime requirement as determined by the Veitch method. The data at hand are too limited to admit of generalization, but they may be worth further consideration.

Greater crop yield on the limed Volusia soil was accompanied by more nitrogen in the drainage water and also by more calcium. On the Dunkirk soil neither of these constituents was found in greater quantity in the drainage water from the limed tanks than from the unlimed. It may be remarked also that analyses of the soil air aspirated from the tanks, as reported in a previous publication,[4] showed no appreciable difference between the limed and the unlimed Dunkirk soil, but in the Volusia soil the carbon-dioxide content of the soil air was much increased by liming.

The fact that nitrate nitrogen in the drainage water and carbon dioxide in the soil air were present in larger amounts in the limed Volusia than in the unlimed gives evidence that decomposition of the organic matter proceeded more rapidly when lime was applied to that soil. This, however, was not the case with the Dunkirk soil, and there is presented the rather unlooked-for situation in which lime increased decomposition of organic matter in one soil but did not do so in the other soil.

A possible explanation for this divergent effect of lime on the two soils is suggested by the quantity of calcium in their respective drainage waters. As before stated, the application of lime had no effect on the removal of calcium in the drainage water from the Dunkirk soil, but it increased markedly the quantity of calcium removed from the Volusia soil. It seems probable that by increasing the concentration of calcium in the soil water, the ammonifying, nitrifying, and other bacteria concerned in decomposition of organic matter were afforded a more congenial environment. If liming did not increase the concentration of calcium in the soil water, as was the case with the Dunkirk soil, there was no acceleration of decomposition.

This experiment would seem to demonstrate one way in which liming may benefit soils. Certainly a larger amount of nitrate nitrogen was placed at the disposal of the plants, and the increased decomposition

[4] Bizzell, J. A., and Lyon, T. L. The effect of certain factors on the carbon-dioxide content of soil air. Amer. Soc. Agron. Journ. **10**: 97–112. 1918.

doubtless rendered other plant nutrients more available by breaking down the compounds in which they were held, as, for instance, the phosphorus of organic matter.

SUMMARY

The object of the experiments here described was to observe the removal, by drainage water and by crops, of calcium and certain other soil constituents from Volusia silt loam. This soil is a rather unproductive type widely distributed over the hills of southern New York. The experiments continued thru a period of five years.

The average annual rainfall for the five years was 32.97 inches. Of the annual rainfall, 27.13 inches, or 82.3 per cent, percolated thru the unplanted soil, and 20.62 inches, or 62.5 per cent, percolated thru the cropped soil. About two-fifths of the rainfall passed into the air from the surface of the soil and thru the plants growing on it.

Application of burnt lime had no appreciable effect on the proportion of rainfall that percolated thru the soil. Similar experiments with Dunkirk soil reported elsewhere gave similar results. Liming either of these soils would probably not facilitate the removal of water thru tile drains.

The average evapo-transpiration ratio for the cropped soils was 1:908, the crops being maize, field peas, oats two years, and barley. The average minimum transpiration ratio for the same crops was 1:451. Both of these ratios were much wider for the Volusia soil of these experiments than for the Dunkirk soil in the experiments previously reported. In this comparison the soil having the greater production of dry matter in crops per unit of water used was the one that had the greater concentration of total solids in the drainage water.

The application of lime apparently favored the production of nitrates in the Volusia soil used in these experiments, while it had no such effect on the Dunkirk soil. The lime requirement of the Dunkirk soil as determined by the Veitch method is very little less than that of the Volusia. The percentage of calcium is about one-third less in the surface foot of the Volusia. In this case the relative calcium content of the soil is a better guide to the need of the soil for lime than is the lime requirement as determined.

The amount of nitrogen in the maize, allowing for that in the roots, added to that in the drainage water from the same tanks, was greater than the amount in the drainage water from the corresponding bare tanks; while

in the case of oats the amount of nitrogen in the crop and in the drainage water was less than in the drainage water from bare soil. The same relation held with the Dunkirk soil.

The quantity of calcium in the drainage water of the unplanted soil was greater than that in the crops and the drainage water combined from the cropped soil. Therefore the process of cropping conserves the calcium in the soil even when the crops are removed. This may be accounted for, in part at least, by the large formation and leaching of nitrates from bare soil.

Apparently the application of burnt lime to the Volusia soil increased the amount of soluble calcium in that soil, but this was not the case with the Dunkirk soil. The Volusia soil has a greater lime requirement and a lower calcium content than has the Dunkirk soil.

To keep the soil supply of calcium up to its present amount would require an annual application of 536 pounds of pure burnt lime, or 957 pounds of pure limestone, to supply the bare soil, and 371 pounds of burnt lime, or 662 pounds of limestone, to supply the planted soil.

Magnesium was present in the drainage water in much smaller quantity than was calcium. Application of lime to the soil increased the quantity of magnesium in the drainage water. Cropping decreased the removal of magnesium from the soil. These relations were the same as for the Dunkirk soil.

Potassium was removed in larger quantity in the drainage water than in the crops, in which respect the Volusia soil differed from the Dunkirk soil. It agreed with the latter, however, in that the application of lime did not increase the quantity of potassium in the drainage water nor in the crops.

Cropping did not materially affect the total removal of sulfur from the soil. Applications of lime resulted in a slight decrease in the sulfur removed in the drainage water. With the Dunkirk soil, applications of lime increased the amount of sulfur removed in the drainage water.

Phosphorus was present in the drainage water only in amounts too small to be determined. Applications of lime increased the removal of phosphorus in the crops. With the Dunkirk soil, applications of lime did not increase the removal of phosphorus in the crops.

Memoir 38, *The Crane-Flies of New York. Part II. Biology and Phylogeny*, the third preceding number in this series of publications, was mailed on July 18, 1921.

Memoir 39, *The Genetic Relations of Plant Colors in Maize*, the second preceding number in this series of publications, was mailed on July 19, 1921.

APPENDIX

TABLE 1. CROP YIELDS FROM LYSIMETER TANKS 13 AND 15 DURING THE PERIOD FROM 1913 TO 1917, EXPRESSED AS DRY MATTER

Year	Tank	Crop	Per tank			Per acre		
			Grain (grams)	Cob (grams)	Straw, stover, or vines (grams)	Grain (bushels)	Cob (tons)	Straw, stover, or vines (tons)
1913	13	Oats	364.2	.....	302.3	62.4	.....	0.83
	15	Oats	337.5	.....	285.5	57.8	.....	0.78
1914	13	Peas	95.6	.....	452.2	8.8	.....	1.24
	15	Peas	172.9	.....	486.5	15.8	.....	1.34
1915	13	Maize	31.2	22.5	746.3	3.0	0.06	2.05
	15	Maize	121.6	68.4	821.8	11.9	0.18	2.26
1916	13	Oats	184.8	.....	266.7	31.6	.....	0.72
	15	Oats	181.0	.....	293.5	31.0	.....	0.80
1917	13	Barley	148.4	.....	161.2	17.0	.....	0.44
	15	Barley	191.0	.....	212.0	21.8	.....	0.58

TABLE 2. FLOW OF DRAINAGE WATER FROM LYSIMETER TANKS 13 TO 16 FROM MAY 1, 1913, TO APRIL 30, 1918

(In liters)

Year and month	Tank			
	13	14	15	16
1913–May	56.8	71.2	70.4	72.0
June	2.4	24.0	3.2	23.2
July	0.0	5.6	0.8	4.8
August	0.4	0.8	0.0	0.0
September	17.6	72.0	0.8	67.2
October	37.6	124.0	26.4	92.0
November	91.6	115.2	79.2	89.6
December	49.2	54.0	44.8	41.6
1914–January	87.6	90.8	116.0	156.4
February	27.2	51.2	38.0	40.4
March	159.2	211.6	206.8	188.0
April	220.8	288.4	215.2	149.2
Totals	750.4	1,108.8	801.6	924.4

TABLE 2 (*continued*)

Year and month	Tank			
	13	14	15	16
1914–May	102.4	130.0	98.4	100.0
June	24.8	59.2	22.4	65.6
July	0.0	23.2	0.4	16.8
August	5.6	220.0	0.0	152.0
September	17.6	64.0	3.2	87.2
October	0.0	2.4	0.0	0.0
November	0.4	19.2	0.0	4.0
December	28.4	55.2	15.6	57.2
1915–January	221.6	278.0	246.8	285.2
February	224.0	179.2	339.6	304.0
March	5.2	2.4	12.0	3.2
April	5.6	1.6	3.2	1.6
Totals	635.6	1,034.4	741.6	1,076.8
1915–May	18.0	25.2	14.4	31.2
June	77.2	85.6	63.2	66.8
July	242.0	292.0	183.6	234.0
August	26.8	114.8	10.0	94.4
September	14.4	75.6	6.0	52.8
October	146.8	178.0	111.2	144.4
November	29.2	43.6	26.4	30.8
December	69.2	67.2	56.0	66.4
1916–January	90.4	86.4	72.8	73.6
February	4.8	8.0	6.4	5.2
March	96.8	143.6	109.6	137.6
April	238.8	268.4	187.6	178.4
Totals	1,054.4	1,388.4	847.2	1,115.6
1916–May to June 5	166.0	165.6	100.4	114.8
June 6				
July				
August	241.6	454.8	224.0	366.0
September				
October				
November				
December	76.8	72.8	85.2	65.6
1917–January 15				
January 16				
February				
March	162.4	142.8	130.0	132.8
April				
Totals	646.8	836.0	539.6	679.2

TABLE 2 (*concluded*)

Year and month	Tank			
	13	14	15	16
1917–May	178.8	194.8	171.6	172.4
June	282.0	345.6	228.0	330.0
July	46.8	80.8	39.6	83.2
August	268.4	296.4	214.0	318.4
September	48.8	62.4	57.6	61.6
October	203.2	219.6	186.0	216.0
November	24.0	20.0	22.4	17.2
December	15.2	17.6	24.8	24.8
1918–January	0.4	0.0	1.2	0.0
February	0.0	64.4	50.8	52.8
March	32.0	73.6	29.2	66.8
April	192.8	143.2	152.8	142.8
Totals	1,292.4	1,518.4	1,178.0	1,486.0
Grand totals	4,379.6	5,886.0	4,108.0	5,282.0

TABLE 3. FLOW OF DRAINAGE WATER FROM LYSIMETER TANKS 13 TO 16 FROM MAY 1, 1913, TO APRIL 30, 1918

(In acre inches)

Period	Tank			
	13	14	15	16
May 1, 1913, to April 30, 1914	18.23	26.94	19.48	22.46
May 1, 1914, to April 30, 1915	15.44	25.13	18.02	26.17
May 1, 1915, to April 30, 1916	25.62	33.74	20.59	27.11
May 1, 1916, to April 30, 1917	15.72	20.31	13.11	16.50
May 1, 1917, to April 30, 1918	31.40	36.90	28.62	36.11
Average annual percolation	21.28	28.60	19.96	25.67

TABLE 4. METEOROLOGICAL RECORDS AT ITHACA, MAY 1, 1913, TO APRIL 30, 1918
Data by months

Year and month	Rainfall (inches)	Temperature (degrees Fahrenheit)			Hours of sunshine	Average hourly velocity of wind (miles)	Mean humidity of air at 8 a. m. (per cent)
		Mean maximum	Mean minimum	Mean			
1913–May	3.15	66.2	44.5	55.4	286.9	9.8	73
June	2.00	78.6	51.4	65.0	332.2	7.5	68
July	1.59	82.5	68.2	70.4	304.7	8.4	69
August	1.92	82.0	57.2	69.6	304.2	8.2	71
September	3.28	73.0	49.2	61.1	219.7	8.1	76
October	3.63	61.3	45.4	53.4	152.5	9.4	86
November	2.21	51.5	35.8	43.6	101.5	11.9	81
December	1.94	39.8	25.3	32.6	84.9	10.0	83
1914–January	1.37	33.7	19.3	26.5	56.7	13.8	85
February	1.62	27.0	8.5	17.8	151.4	11.6	82
March	1.90	39.1	24.3	31.7	141.7	10.3	82
April	4.35	51.1	33.1	42.1	144.8	11.6	78
May	3.63	71.1	47.5	59.3	297.7	8.1	71
June	4.75	76.5	54.5	65.5	301.2	8.5	74
July	1.89	81.2	59.2	70.2	230.8	7.0	78
August	6.10	80.2	58.2	69.2	208.4	7.0	80
September	1.96	71.1	48.2	59.6	255.2	7.6	82
October	1.38	63.6	43.9	53.8	212.5	8.7	86
November	0.68	46.4	31.1	38.8	111 9	12.5	78
December	2.70	32.9	19.1	26.0	73.3	10.4	82
1915–January	5.02	33.4	19.7	26.6	96.0	10.4	85
February	1.83	37.8	22.7	30.2	94.1	11.9	86
March	0.32	37.5	21.9	29.7	183.5	10.9	83
April	0.55	62.7	39.6	51.2	202.2	9.0	70
May	2.44	61 6	41.6	51.6	187.7	8.4	74
June	3.94	75.7	51.6	63.6	273.4	8.4	69
July	6.18	80.2	58.2	69.2	212.8	6.3	82
August	3.70	75.0	57.5	66.2	174.0	7.9	86
September	2.58	75.6	54.1	64.8	203.6	7.9	86
October	4.10	59.9	43.7	51.8	155.8	9.4	83
November	1.10	47.7	33.1	40.4	107.9	12.1	78
December	2.90	33.6	23.3	28.4	42.6	12.0	84
1916–January	0.81	40.0	23.7	31.8	73.7	12.2	80
February	2.97	30.1	13.0	21.6	87.8	10.1	83
March	2.28	35.3	18.7	27.0	162.5	10.9	81
April	2.77	53.7	37.0	45.4	133.4	8.4	80
May	4.27	68.4	46.9	57.6	189.2	10.6	71
June	3.48	70.9	51.9	61.4	171.0	9.8	79
July	1.29	85.8	63.5	74.6	226.7	7.8	77
August	1.50	83.7	58.7	71.2	283.2	7.3	75
September	5.65	72.8	50.9	61.8	232.7	9.5	73
October	1.59	63.1	39.6	51.4	180.5	9.7	74
November	1.53	46.7	31.4	39.0	88.5	10.2	77
December	1.01	35.9	22.0	29.0	99.9	12.1	79

TABLE 4 (*continued*)

Year and month	Rainfall (inches)	Temperature (degrees Fahrenheit)			Hours of sunshine	Average hourly velocity of wind (miles)	Mean humidity of air at 8 a. m. (per cent)
		Mean maximum	Mean minimum	Mean			
1917–January	1.82	34.1	17.7	25.9	101.8	12.9	84
February	0.70	29.6	10.4	20.0	99.1	13.5	86
March	1.59	41.9	25.9	33.9	127.1	14.2	78
April	1.83	52.4	35.5	44.0	140.9	10.9	75
May	4.41	56.7	40.0	48.4	107.9	10.6	72
June	7.35	74.1	53.6	63.8	167.8	8.0	76
July	3.25	81.4	61.6	71.5	250.8	7.5	76
August	8.45	79.9	58.5	69.2	244.8	7.5	80
September	2.22	69.9	47.2	58.6	231.2	7.6	82
October	4.84	53.6	36.7	45.2	77.8	10.8	81
November	0.64	43.3	26.4	34.8	93.6	9.6	81
December	2.48	26.9	10.7	18.8	72.2	12.1	82
1918–January	1.83	22.0	6.8	14.4	127.0	10.9	79
February	1.48	35.0	13.7	24.4	104.8	14.6	77
March	2.58	48.2	25.3	36.8	178.6	11.3	73
April	3.54	56.3	35.2	45.8	171.2	10.3	75

Average of each month

Month	Rainfall (inches)	Temperature (degrees Fahrenheit)			Hours of sunshine	Average hourly velocity of wind (miles)	Mean humidity of air at 8 a. m. (per cent)
		Mean maximum	Mean minimum	Mean			
May	3.58	64.8	44.1	54.5	213.9	9.5	72.2
June	4.30	75.2	52.6	63.9	249.1	8.4	73.2
July	2.84	82.2	62.1	71.2	245.2	7.4	76.4
August	4.33	80.2	58.0	69.1	242.9	7.6	78.4
September	3.14	72.5	49.9	61.2	228.5	8.1	79.8
October	3.11	60.3	41.9	51.1	155.8	9.6	82.0
November	1.23	47.1	31.6	39.3	100.7	11.3	79.0
December	2.21	33.8	20.1	26.96	74.6	11.3	82.0
January	2.17	32.6	17.4	25.0	91.0	12.0	82.6
February	1.72	31.9	13.7	22.8	107.4	12.3	82.8
March	1.73	40.4	23.2	31.8	158.7	11.5	79.4
April	2.60	55.2	36.1	45.7	158.5	10.0	75.6

TABLE 4 (*concluded*)
Data by years

Year	Total rainfall (inches)	Temperature (degrees Fahrenheit)			Total hours of sunshine	Average hourly velocity of wind (miles)	Mean humidity of air at 8 a. m. (per cent)
		Mean maximum	Mean minimum	Mean			
May 1913, to April 1914	28.96	57.2	38.5	47.4	2,281.2	10.1	77.8
May 1914, to April 1915	30.81	57.9	38.8	48.3	2,266.8	9.3	79.6
May 1915, to April 1916	35.77	55.7	37.9	46.8	1,815.2	9.5	80.5
May 1916, to April 1917	26.26	57.1	37.9	47.5	1,940.6	10.7	77.3
May 1917, to April 1918	43.07	53.9	34.6	44.3	1,827.7	10.1	77.8

TABLE 5. SUBSTANCES CONTAINED IN DRAINAGE WATER, IN PARTS PER MILLION

	Tank			
	13	14	15	16
1913–14	TOTAL SOLIDS			
May 1–September 30	246	314	237	422
October 1–April 30	177	220	199	310
1914–15				
May 1–September 30	241	245	223	370
October 1–April 30	200	179	184	252
1915–16				
May 1–September 30	302	271	309	363
October 1–April 30	260	228	263	292
1916–17				
May 1–April 30	296	270	325	353
1917–18				
May 1–April 30	285	369	295	306
Averages	251	262	254	333.5
1913–14	NITRATES			
May 1–September 30	40.0	66.0	42.0	116.0
October 1–April 30	8.7	50.8	19.2	68.3
1914–15				
May 1–September 30	6.0	30.7	14.6	55.4
October 1–April 30	7.6	22.9	22.2	42.2
1915–16				
May 1–September 30	20.6	42.0	25.3	57.3
October 1–April 30	8.0	18.5	7.8	27 3
1916–17				
May 1–April 30	6.5	36.0	5.8	60.0
1917–18				
May 1–April 30	3.0	20.5	3.0	25.0
Averages	12.56	35.93	17.48	56.44

TABLE 5 (*continued*)

	Tank			
	13	14	15	16
	BICARBONATES			
1913–14				
May 1–September 30	170	197	169	213
October 1–April 30	142.3	126.8	153.8	146.8
1914–15				
May 1–September 30	170	163	168.75	207
October 1–April 30	161.1	131.5	127.3	135
1915–16				
May 1–September 30	200	171.5	226.5	251
October 1–April 30	212.5	153	201.5	206.5
1916–17				
May 1–April 30	244.3	194.5	288.8	246.8
1917–18				
May 1–April 30	255	217	280	234
Averages	194.4	169.29	201.96	205.01
	SULFATES			
1913–14				
May 1–September 30	23	33	39	57
October 1–April 30	22.8	15.9	18.3	15.5
1914–15				
May 1–September 30	10.6	7.1	13.9	8 0
October 1–April 30	17.2	23.4	12.2	14.3
1915–16				
May 1–September 30	36.0	22.6	22.4	22.9
October 1–April 30	34.8	26.3	33.0	23 0
1916–17				
May 1–April 30	34.5	27.0	34.5	27.0
1917–18				
May 1–April 30	21.5	16.3	19.4	19.2
Averages	25.05	21.46	24 09	23.36
	SILICA			
1913–14				
May 1-September 30	5.6	6.3	5.8	6.8
October 1–April 30	7.1	5.9	8.4	8.9
1914–15				
May 1–September 30	6.6	9.4	5.4	12.0
October 1–April 30	6.6	4.5	5.5	5.4
1915–16				
May 1–September 30	8.9	8.0	8.6	10.5
October 1–April 30	5.5	4.9	7.6	5.5
1916–17				
May 1–April 30	9.0	8.7	10.3	7.6
1917–18				
May 1–April 30	11.8	11.4	10.3	10.2
Averages	7.64	7.39	7.74	8.36

TABLE 5 (*continued*)

	Tank			
	13	14	15	16
	PHOSPHATES			
1913–14				
May 1–September 30	None	None	None	None
October 1–April 30	.....	.....	.....	.....
1914–15				
May 1–September 30	Trace	Trace	None	Trace
October 1–April 30	Trace	Trace	Trace	Trace
1915–16				
May 1–September 30	None	None	None	None
October 1–April 30	None	None	None	None
1916–17				
May 1–April 30	Trace	Trace	Trace	Trace
1917–18				
May 1–April 30	None	None	None	None
	CALCIUM			
1913–14				
May 1–September 30	38.5	56.3	40.9	70.8
October 1–April 30	42.2	49.8	49.7	62.4
1914–15				
May 1–September 30	46.1	49.0	47.5	77.2
October 1–April 30	65.3	37.8	43.8	52.8
1915–16				
May 1–September 30	52.8	50.8	64.7	71.0
October 1–April 30	49.3	41.0	50.1	62.1
1916–17				
May 1–April 30	58.1	52.9	71.7	77.5
1917–18				
May 1–April 30	56.6	54.2	63.1	64.4
Averages	51.12	48.99	53.95	67.28
	MAGNESIUM			
1913–14				
May 1–September 30	5.8	7.6	6.8	9.0
October 1–April 30	6.3	6.7	6.9	9.4
1914–15				
May 1–September 30	5.6	6.0	6.0	9.2
October 1–April 30	4.5	4.2	3.6	5.4
1915–16				
May 1–September 30	7.8	7.6	7.9	3.6
October 1–April 30	6.7	5.1	8.3	8.1
1916–17				
May 1–April 30	6.6	8.5	9.6	11.0
1917–18				
May 1–April 30	5.8	6.1	7.1	7.9
Averages	6.15	6.48	7.04	9.22

TABLE 5 (*concluded*)

	Tank			
	13	14	15	16
	POTASSIUM			
1913–14				
May 1–September 30	12.4	9.5	11.3	13.8
October 1–April 30	8.3	8.3	6.1	7.1
1914–15				
May 1–September 30	16.1	16.9	11.5	12.2
October 1–April 30	8.9	8.6	5.0	6.0
1915–16				
May 1–September 30	29.7	21.6	20.7	17.2
October 1–April 30	18.9	13.8	14.3	9.9
1916–17				
May 1–April 30	22.6	18.7	17.4	14.4
1917–18				
May 1–April 30	22.2	18.6	16.7	15.1
Averages	17.40	14.51	12.87	11.96
	SODIUM			
1913–14				
May 1–September 30	15.6	12.9	11.3	10.2
October 1–April 30	22.9	22.5	24.0	22.6
1914–15				
May 1–September 30	17.5	13.9	12.7	16.7
October 1–April 30	22.9	17.9	17.8	15.2
1915–16				
May 1–September 30	24.5	19.8	19.9	20.7
October 1–April 30	26.0	18.9	24.9	18.9
1916–17				
May 1–April 30	18.4	13.7	18.5	13.6
1917–18				
May 1–April 30	18.7	14.4	16.9	13.7
Averages	20.83	16.77	18.25	16.45
	CARBONATES			
1913–14				
May 1–September 30	None	None	None	None
October 1–April 30	None	None	None	None
1914–15				
May 1–September 30	3.68	Trace	Trace	4.92
October 1–April 30	None	None	None	None
1915–16				
May 1–September 30	7.62	6.40	None	7.37
October 1–April 30	7.84	4.41	9.31	4.90
1916–17				
May 1–April 30	None	None	None	None
1917–18				
May 1–April 30	None	None	None	None
Averages	2.39	1.35	1.16	2.15

TABLE 6. SUBSTANCES CONTAINED IN DRAINAGE WATER, IN POUNDS PER ACRE

	Tank			
	13	14	15	16
	TOTAL SOLIDS			
1913–14				
May 1–September 30	104.1	299.2	97.6	387.9
October 1–April 30	656.7	1,133.9	796 7	1,293.7
Totals	760.8	1,433.1	894.3	1,681.6
1914–15				
May 1–September 30	198.9	669.4	152.0	857.9
October 1–April 30	534.4	530.6	625.4	909.1
Totals	733.3	1,200.0	777.4	1,767.0
1915–16				
May 1–September 30	629.6	885.7	471.9	958.4
October 1–April 30	968.4	999.0	826.0	1,023.9
Totals	1,598.0	1,884.7	1,297.9	1,982.3
1916–17				
May 1–April 30	1,054.9	1,243.7	966.2	1,322.6
1917–18				
May 1–April 30	2,028.0	1,986.5	1,914.6	2,505.3
Yearly averages	1,235.0	1,549.6	1,170.1	1,851.7
	NITRATES			
1913–14				
May 1–September 30	16.5	62.8	17.1	106.3
October 1–April 30	32.4	261.8	76.8	285.1
Totals	48.9	324.6	93.9	391.4
1914–15				
May 1–September 30	4.9	83.7	9.9	128.4
October 1–April 30	20.4	67.7	75.5	90.9
Totals	25.3	151.4	85.4	219.3
1915–16				
May 1–September 30	42.9	137.2	38.6	151.2
October 1–April 30	29.8	81.0	24.5	95.7
Totals	72.7	218.2	63.1	246.9
1916–17				
May 1–April 30	23.1	165.8	17.2	224.8
1917–18				
May 1–April 30	20.9	171.3	19.3	204.4
Yearly averages	38.2	206.2	55.8	257.3

TABLE 6 (*continued*)

	Tank			
	13	14	15	16
	BICARBONATES			
1913–14				
May 1–September 30	71.6	187.3	69.4	195.6
October 1–April 30	527.9	653.5	615.7	612.6
Totals	599.5	840.8	685.1	808.2
1914–15				
May 1–September 30	140.5	445.2	115.1	479.9
October 1–April 30	430.3	389.5	432.5	487.1
Totals	570.8	834.7	547.6	967.0
1915–16				
May 1–September 30	417.0	560.5	345.9	662.7
October 1–April 30	791.5	670.3	632.8	724.1
Totals	1,208.5	1,230.8	978.7	1,386.8
1916–17				
May 1–April 30	870.6	895.9	858.6	924.7
1917–18				
May 1–April 30	1,814.9	1,814.9	1,817.2	1,915.9
Yearly averages	1,012.8	1,123.4	977.4	1,200.5
	SULFATES			
1913–14				
May 1–September 30	9.3	31.4	15.9	52.3
October 1–April 30	84.6	81.9	73.2	64.7
Totals	93.9	113.3	89.1	117.0
1914–15				
May 1–September 30	8.8	19.2	9.3	18.1
October 1–April 30	45.7	68.8	41.3	51.2
Totals	54.5	88.0	50.6	69.3
1915–16				
May 1–September 30	75.0	73.8	34.2	60.4
October 1–April 30	129.6	115.2	103.6	80.6
Totals	204.6	189.0	137.8	141.0
1916–17				
May 1–April 30	122.9	123.3	102.5	101.1
1917–18				
May 1–April 30	152.6	136.1	125.6	157.0
Yearly averages	125.7	129.9	101.1	117.1

TABLE 6 (*continued*)

	Tank			
	13	14	15	16
	SILICA			
1913–14				
May 1–September 30	2.2	6.0	2.2	6.0
October 1–April 30	26.3	30.4	33.6	37.1
Totals	28.5	36.4	35.8	43.1
1914–15				
May 1–September 30	5.5	25.3	3.3	27.5
October 1–April 30	17.6	13.2	18.7	19.3
Totals	23.1	38.5	22.0	46.8
1915–16				
May 1–September 30	18.5	26.1	13.1	27.7
October 1–April 30	20.5	21.4	23.8	19.3
Totals	39.0	47.5	36.9	47.0
1916–17				
May 1–April 30	32.0	40.3	31.8	24.4
1917–18				
May 1–April 30	83.7	95.3	66.6	83.2
Yearly averages	41.2	51.6	38.6	48.9
	CALCIUM			
1913–14				
May 1–September 30	15.9	53.4	16.5	65.0
October 1–April 30	156.4	256.8	198.9	260.4
Totals	172.3	310.2	215.4	325.4
1914–15				
May 1–September 30	38.0	133.9	32.5	179.0
October 1–April 30	174.1	111.8	148.7	190.6
Totals	212.1	245.7	181.2	369.6
1915–16				
May 1–September 30	110.0	165.0	98.9	187.6
October 1–April 30	183.8	179.8	157.5	217.7
Totals	293.8	344.8	256.4	405.3
1916–17				
May 1–April 30	207.0	243.6	213.1	290.3
1917–18				
May 1–April 30	402.8	452.9	409.4	526.7
Yearly averages	257.6	319.4	255.1	383.4

TABLE 6 (*continued*)

	Tank			
	13	14	15	16
	MAGNESIUM			
1913–14				
May 1–September 30	2.2	7.1	2.7	8.2
October 1–April 30	23.4	34.5	27.6	39.4
Totals	25.6	41.6	30.3	47.6
1914–15				
May 1–September 30	4.4	15.9	3.8	20.9
October 1–April 30	12.1	12.1	12.1	19.3
Totals	16.5	28.0	15.9	40.2
1915–16				
May 1–September 30	16.3	25.0	12.1	36.0
October 1–April 30	24.9	22.3	26.0	28.5
Totals	41.2	47.3	38.1	64.5
1916–17				
May 1–April 30	23.5	39.1	28.5	41.2
1917–18				
May 1–April 30	41.3	50.7	45.7	64.4
Yearly averages	29.6	41.3	31.7	51.6
	POTASSIUM			
1913–14				
May 1–September 30	4.9	8.8	4.4	12.6
October 1–April 30	30.9	42.8	24.2	29.8
Totals	35.8	51.6	28.6	42.4
1914–15				
May 1–September 30	13.2	46.3	7.7	28.1
October 1–April 30	23.1	25.3	16.5	21.5
Totals	36.3	71.6	24.2	49.6
1915–16				
May 1–September 30	61.9	70.7	31.6	45.4
October 1–April 30	70.5	60.4	44.9	34.7
Totals	132.4	131.1	76.5	80.1
1916–17				
May 1–April 30	80.5	86.1	51.7	53.9
1917–18				
May 1–April 30	158.1	155.4	108.0	123.4
Yearly averages	88.6	99.1	57.8	69.9

TABLE 6 (*concluded*)

	Tank			
	13	14	15	16
1913–14	SODIUM			
May 1–September 30	6.6	12.1	4.4	9.3
October 1–April 30	85.1	116.1	95.9	94.4
Totals	91.7	128.2	100.3	103.7
1914–15				
May 1–September 30	14.3	38.0	8.2	15.4
October 1–April 30	61.1	52.9	60.6	54.5
Totals	75.4	90.9	68.8	69.9
1915–16				
May 1–September 30	51.2	64.8	30.4	46.6
October 1–April 30	96.8	83.0	78.2	66.2
Totals	148.0	147.8	108.6	112.8
1916–17				
May 1–April 30	65.5	63.1	55.0	50.9
1917–18				
May 1–April 30	132.8	120.1	109.6	111.8
Yearly averages	102.7	110.0	88.4	89.8

TABLE 7. ASH AND ASH CONSTITUENTS IN CROPS, BY YEARS
(In percentage of dry matter)

Year	Tank	Crop	Part of crop	Ash	Ca	Mg	K	S	P
1913	13	Oats	Grain	3.67	0.03	0.06	0.62	0.24	0.56
	13	Oats	Straw	6.92	0.43	0.12	2.40	0.18	0.12
	15	Oats	Grain	3.39	0.04	0.03	0.62	0.23	0.56
	15	Oats	Straw	6.61	0.42	0.17	2.16	0.23	0.11
1914	13	Peas	Grain	4.30	0.05	0.04	1.15	0.36	0.48
	13	Peas	Straw	27.43	0.67	0.23	0.46	0.62	0.33
	15	Peas	Grain	3.43	0.04	0.04	1.14	0.33	0.48
	15	Peas	Straw	14.20	0.99	0.18	0.04	0.60	0.35
1915	13	Maize	Grain	1.74	0.03	0.09	0.38	0.30	0.36
	13	Maize	Straw	6.54	0.15	0.08	1.19	0.30	0.22
	15	Maize	Grain	1.60	0.06	0.07	0.42	0.18	0.37
	15	Maize	Straw	5.19	0.13	0.11	0.83	0.31	0.22
1916	13	Oats	Grain	3.33	0.02	0.03	0.77	0.19	0.47
	13	Oats	Straw	8.16	0.28	0.12	2.49	0.30	0.19
	15	Oats	Grain	3.88	0.01	0.04	0.67	0.18	0.52
	15	Oats	Straw	7.89	0.32	0.20	2.19	0.30	0.24
1917	13	Barley	Grain	3.01	0.03	0 02	0.54	0.21	0.52
	13	Barley	Straw	7.41	0.24	0.07	1.03	0.24	0.20
	15	Barley	Grain	2.92	0.02	0.03	0.58	0.20	0.50
	15	Barley	Straw	6.13	0.33	0.04	0.93	0.24	0.24

TABLE 8. ASH AND ASH CONSTITUENTS IN CROPS, BY YEARS
(In pounds per acre)

Year	Tank	Crop	Part of crop	Ash	Ca	Mg	K	S	P
1913	13	Oats	Grain	70.8	0.5	1 1	11.9	4.6	10 9
	13	Oats	Straw	116.9	7.3	2.0	40.5	3.1	2.0
	13	Oats	Total	187.7	7.8	3.1	52.4	7.7	12.9
	15	Oats	Grain	62.7	0.8	0.6	11.3	4.2	10.3
	15	Oats	Straw	103.2	6.1	2.6	33.7	3.5	1.7
	15	Oats	Total	165.9	6.9	3.2	45.0	7.7	12.0
1914	13	Peas	Grain	21.5	0.3	0.2	5.8	1.9	2.4
	13	Peas	Straw	679.5	16.5	5.7	11.3	5.5	8.2
	13	Peas	Total	701.0	16.8	5.9	17.1	17.4	10.6
	15	Peas	Grain	31.6	0.4	0.4	10.4	3.0	4.4
	15	Peas	Straw	391.2	27.4	4.9	11.4	16.6	9.6
	15	Peas	Total	422.8	27.8	5.3	21.8	19.6	14.0
1915	13	Maize	Grain	2.9	0.1	0.2	0.7	0.6	0.6
	13	Maize	Straw	264.8	6.0	3.2	47.9	12.0	9.0
	13	Maize	Total	267.7	6.1	3.4	48.6	12.6	9.6
	15	Maize	Grain	10.6	0.5	0.4	2.8	1.2	2.5
	15	Maize	Straw	231.7	5.7	4.9	37.2	13.6	9.9
	15	Maize	Total	242.3	6.2	5.3	40.0	14.8	12.4
1916	13	Oats	Grain	33.7	0.2	0.3	7.8	2.0	4.8
	13	Oats	Straw	118.1	4.1	1.8	36.1	4.3	2.8
	13	Oats	Total	151.8	4.3	2.1	43.9	6.3	7.6
	15	Oats	Grain	38.5	0.1	0.4	6.7	1.8	5.2
	15	Oats	Straw	126.1	5.3	3.3	35.1	4.8	3.8
	15	Oats	Total	164.6	5.4	3.7	41.8	6.6	9.0
1917	13	Barley	Grain	24.7	0.2	0.2	4.4	1.8	4.3
	13	Barley	Straw	65.6	2.2	0.7	9.1	2.1	1.8
	13	Barley	Total	90.3	2.4	0.9	13.5	3.9	6.1
	15	Barley	Grain	30.7	0.2	0.3	6.1	2.1	5.3
	15	Barley	Straw	72.9	3.9	1.7	11.0	2.9	2.9
	15	Barley	Total	103.6	4.1	2.0	17.1	5.0	8.2

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BEAN ANTHRACNOSE

MORTIER F. BARRUS

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CONTENTS

PAGE

The host 101
The disease 104
Economic aspects 104
Name, history, and geographical distribution 104
Economic importance 106
Symptomatic aspects 107
On the seed 107
On the seedlings 108
On the leaves 108
On the roots and other parts 108
On the pods 110
Etiologic aspects 112
Name, classification, and synonymy of the causal organism 112
Morphology and physiology 116
Spores 116
Spore germination 117
Mycelium and spore production in culture 120
The ascogenous stage 124
Relation of fungus to host 126
Penetration of the host 126
Reproduction of the fungus within the host 128
The fungus in the seed 129
Infection of the seedling from affected seed 131
Longevity of fungus in soil 132
Further infection of the plant and spread of the disease through the field 144
Infection of seeds 146
Infection studies 147
Susceptibility of plants of different ages to infection 147
Susceptibility of different parts of the plant to infection 148
Susceptibility of different varieties of *Phaseolus vulgaris* L. to infection 148
Susceptibility of other species of the genus Phaseolus to infection 152
Susceptibility of plants of other genera and families to infection. 153
Susceptibility of *Phaseolus vulgaris* to infection from other anthracnose fungi 157
Ecologic aspects 159
Prophylactic aspects 164
Seed disinfection 164
Sorting out affected seed 168

PAGE
Selecting seed from clean pods 168
Procuring seed from localities where anthracnose does not occur. 175
Avoiding conditions favorable for the dissemination and growth of the fungus 176
Manner of planting 177
Good land drainage 178
Removal of affected seedlings 178
Leaving the plants untouched while wet 179
Destroying diseased vines in the fall 179
Planting at a time of the year when anthracnose is least likely to be present 180
Planting early-maturing varieties 180
Spraying 180
Applying a fungicide to picked pods before shipping 193
Application of a fungicide to the soil 193
Rotation of crops 194
Selection of resistant plants 194
Consideration of prophylactic measures 195
Summary 197
Literature cited 199

BEAN ANTHRACNOSE

BEAN ANTHRACNOSE

MORTIER F. BARRUS

THE HOST

Next to the potato and the sweet potato, the bean (considered as a vegetable) is the most important crop grown in this country. Not only are beans grown in practically every home garden, but they are of great commercial importance also. The United States Census Bureau (1913a) reports the production of dry edible beans grown for commercial purposes in this country during 1909 as 11,251,160 bushels, or more than double that of 1899, representing a value of $21,771,482. The Monthly Crop Report of the United States Department of Agriculture (1917: 133) estimates the production for 1916 as 12,029,000 bushels; for 1917 it was 18,129,000 bushels, the culture of beans having been stimulated by the demand and by the high prices paid as a result of the war. Since the war there has been a marked reduction in area in the States having a high bean production. Dry beans are a staple crop in New York, Michigan, Colorado, New Mexico, California, and several other States, while string beans are grown extensively in many parts of the country as a truck crop. In northern New York, in Michigan, Colorado, and California, and in southern Canada, the production of garden and field beans for seed has developed into a large and profitable industry. Large areas also are devoted to the production of snap beans for canning.

Prior to 1899, New York was the leading State in the production of dry edible beans, in 1879 producing 42.4 per cent of the total crop in the United States and in 1889 producing 35.1 per cent. In 1909, however, it produced only about 15 per cent of the total crop (U. S. Census Bureau, 1913a). While production has greatly increased in the other large bean-producing States (table 1), New York has lagged behind, although it was stirred on somewhat during 1917 and 1918.[1] Low yields resulting from disease and from poor weather conditions inevitably resulted in reduced acreage for 1919.

[1] Data for 1879 and 1889 were obtained from the Eleventh Census; for 1899 and 1909, from the Thirteenth Census; for 1914, from the Monthly Crop Report for 1916; for 1915, 1916, and 1917, from the Monthly Crop Report for 1917; for 1918, from the Monthly Crop Report for 1918; for 1919, from the Monthly Crop Reporter for 1919; for 1920, from the Monthly Crop Reporter for 1920. These references are given under *Literature Cited*, page 199.

TABLE 1. ACREAGE AND PRODUCTION (IN BUSHELS) SINCE 1879, OF DRY EDIBLE BEANS IN THE FIVE LARGEST BEAN-PRODUCING STATES AND IN THE UNITED STATES

Year		New York	Michigan	California	Colorado	New Mexico	United States
1879	Production...	1,303,444	167,658	378,971	.....	16,168	3,075,050
1889	Production...	1,111,510	434,014	713,480	7,265	7,843	3,163,554
1899	Acreage.....	129,298	167,025	45,461	2,406	17,417	453,841
	Production...	1,360,445	1,806,413	658,515	28,570	36,022	5,064,490
1909	Acreage.....	115,698	403,669	157,987	5,040	20,766	802,991
	Production...	1,681,506	5,282,511	3,328,218	53,926	85,795	11,251,160
1914	Acreage.....	118,000	490,000	215,000	20,000	32,000	.....
	Production...	1,650,000	5,488,000	3,875,000	300,000	272,000	.....
1915	Acreage.....	130,000	506,000	225,000	21,000	46,000	.....
	Production...	1,495,000	4,250,000	3,868,000	340,000	368,000	.....
1916	Acreage.....	190,000	470,000	340,000	38,000	64,000	1,244,000
	Production...	1,140,000	3,102,000	5,576,000	424,000	425,000	12,029,000
1917	Acreage.....	210,000	639,000	558,000	193,000	213,000	2,117,200
	Production...	1,575,000	3,514,000	8,035,000	1,467,000	958,000	18,129,000
1918	Acreage.....	200,000	543,000	592,000	252,000	149,000	.....
	Production...	1,660,000	4,887,000	8,880,000	1,638,000	596,000	.....
1919	Acreage.....	90,000	300,000	400,000	69,000	123,000	.....
	Production...	1,305,000	4,140,000	5,000,000	448,000	922,000	.....
1920	Acreage.....	90,000	275,000	285,000	63,000	121,000	.....
	Production...	1,260,000	3,575,000	2,850,000	504,000	811,000	.....

The figures in table 2, taken from statistics compiled by order of the New York State Food Commission (1919), give the acreage and production during 1917 of important bean-growing counties in the State and show the location of the bean area. A larger yield to the acre was obtained by some of the other counties which planted a smaller acreage.

TABLE 2. ACREAGE AND PRODUCTION OF FIELD BEANS IN THE TEN LARGEST-PRODUCING COUNTIES OF NEW YORK STATE IN 1917

County	Acreage	Production (bushels)
Livingston	37,010	325,245
Wyoming	23,146	200,949
Genesee	18,835	101,158
Ontario	13,884	82,353
Wayne	12,615	86,105
Monroe	11,076	42,751
Orleans	9,640	38,561
Erie	9,235	46,547
Yates	9,007	70,442
Schuyler	8,164	59,650
New York State	218,742	1,477,061

New York ranks first of all the States in the amount and value of canned string beans, the United States Census Bureau (1913b) reporting 452,634 cases having a value of $839,135, or more than half the total value for the entire country. It is assumed that nearly all string beans canned in the States were grown within its territory.

It is thus seen that the bean industry in New York and in the country at large is an important one, and well worthy any attention that may be given to it by the Federal Government and by the various experiment stations.

The common bean (*Phaseolus vulgaris* L.) becomes affected at times by various diseases, among which the bean anthracnose is an important one in New York State. Bacterial blight also occurs frequently on the common bean and on the lima bean (*P. lunatus* L.), and was severe in 1916 and 1917. Root rots — especially the one caused by *Fusarium Martii phaseoli*, though black root rot, caused by *Thielavia basicola* Zopf., should be mentioned also — are causing considerable loss in restricted localities and may be more prevalent than is generally known. Rhizoctonia stem canker and pod spot, caused by *Corticium vagum* B. & C., has been reported from a few places as being serious and is known to have a general distribution. Bean rust, caused by *Uromyces appendiculatus* (Pers.) Lév., occurs occasionally, but does little damage in this State though it is severe at times in the South and the West. Brown rot, caused by *Sclerotinia libertiana* Fuckel, is destructive only during periods of extended rains and warm weather, and then only on vines so bushy that they do not permit good aëration. The leaf spot caused by *Phyllosticta* sp. is uncommon in the State, while leaf spot caused by *Isariopsis griseola* Sacc. has not been reported here.

In addition to the parasitic diseases just mentioned, mosaic, supposed to be due to a filterable virus, should certainly be included because of its general prevalence in the State and its apparently serious effect.

The writer has devoted more or less of his time for the past ten years to the study of the anthracnose disease and the manner of its control. In the following pages he presents his opinions and those of others in regard to the disease, and records the results of his experiments.

THE DISEASE

ECONOMIC ASPECTS

Name, history, and geographical distribution

The name *bean anthracnose*, generally applied by American, English, French, Italian, and other pathologists to the disease under consideration, was apparently first used in this connection by Scribner (1888), although the name *anthracnose* was used earlier to designate the grape disease caused by *Gloeosporium ampelophagum* Sacc. The terms *pod spot*, or *canker*, and *leaf spot* are sometimes applied to the disease as it occurs on these respective parts of the plant; while not uncommonly the terms *rust* and *blight*, and rarely *scab*, are erroneously used by laymen. Frank (1883 b) called the disease *Fleckenkrankheit*, and the names *Brennerflecken*, *Brennerfleckenkrankheit*, *Brennfleckenkrankheit*, and *Schwarzfleckenkrankheit* have been used by German writers. In Holland, Schenk (1917) speaks of the disease as *Vlekziekte*, and in Denmark it is called *Bonnesyge* by Lind (1910).

The disease was first definitely described by Saccardo (1878), who reported its discovery by Lindemuth in the fruit and vegetable garden of the Agricultural Institute of Poppelsdorf, at Bonn, in August, 1875. Anthracnose spots are present, however, on specimens of bean pods distributed by Desmazières (1843 b) under the name *Septoria leguminum* Nob. Berkeley (1880) reports the disease on kidney beans from Bedford, England, ascribing it to Ascochyta. Saccardo (1881) shows a good colored reproduction of a pod affected with anthracnose, and drawings of the fructifications of the fungus. The label indicates that the fungus was collected at Padua in June, 1875, on *Phaseolus vulgaris*. Frank (1883 b) states that Lindemuth reported to him the occurrence of the disease in 1875 on the red-mottled Zucker-Stangenbrechbohnen, and a few years later on numerous other varieties grown in the same vicinity. Frank himself says the disease occurred in other parts of Germany in 1881 and in various localities in 1882, it being especially severe the latter year. He gives an excellent account of the disease and its cause in the article cited. Saccardo (1884) mentions the disease as being common and injurious in Germany, Italy, France, England, and North America. Richon (1889) records its presence in the Marne district of France.

Ellis and Everhart (1885:111) report Dr. Farlow's observations of the common occurrence of this fungus on beans in the Cambridge (Massachusetts) market since 1882. From the Plant Disease Bulletin issued by the Plant Disease Survey of the United States Plant Industry Bureau (1918:254), it appears that the disease was reported from Pennsylvania, Maryland, and Louisiana in 1887; from Michigan in 1889; and from New York and Ohio in 1890. Scribner (1888:361), after speaking of its distribution in Europe, says that specimens have been received from Maine, Massachusetts, Wisconsin, Pennsylvania, Louisiana, and the District of Columbia.

Since then the disease has been reported from a number of places in Germany, Italy, England, and the United States. Reports of its existence — some recording only its presence and others its prevalence and destructiveness — have been recorded from Norway (Schoyen, 1901), Sweden (Eriksson, 1889), Denmark (Lind, 1910), Russia (Jaczewski, 1912), Tyrol (Bubák and Kabát, 1904), Belgium (Marchal, 1907), Holland (Sprenger, 1918), Ireland (Schoebotham, 1909), Japan (Ideta, 1911), Formosa (Fujikuro, 1914), India (Butler, 1918), Transvaal (Pole-Evans, 1907), Australia (Cooke, 1892), New Zealand (Kirk, 1905), Argentina (Spegazzini, 1899), Brazil (Puttemans, 1901), Cuba (Cook and Horne, 1908), Alaska (Anderson, 1916), and Canada (Craig, 1893).

From the bulletin issued by the Plant Disease Survey (U. S. Plant Industry Bureau, 1918) and from the earlier survey reports by Orton and by Orton and Ames (1904–1909), as well as from the bulletins and reports of the various experiment stations in this country, it appears that the disease has occurred at one time or another in every State in the Union except South Dakota, Wyoming, and Nevada. Doubtless it has occurred in these three States also but has not been reported.

It is thus seen that the disease is world-wide in its distribution, occurring in nearly every place where beans are grown. The climatic condition of a country or a region has much to do with the development of the disease, so that in some of the countries where it has been reported it is of no importance and in others it becomes a serious pest. While it has been reported from Alaska, it cannot be enphytotic there, as seed of *Phaseolus vulgaris* will not mature in that latitude; but the summer climate of Alaska is not unfavorable for the development of the fungus when introduced in imported seed affected by it.

Economic importance

While bean anthracnose can be found on some plants year after year, it is only during certain periods most favorable for its development that it becomes widespread and causes serious loss. Such epiphytotics are coincident with or closely follow periods of rather abundant rainfall during the growing season, and often recur in three or more successive years. Frank (1883b:512), as already noted, reports such an epiphytotic in Germany in 1882, Querner (1908) reports one in 1908, and Fischer (1919:246) reports epiphytotics in 1915 and 1916. Voglino (1892) reports a complete destruction of the crop in 1891 in several localities in Italy.

Beach (1892:308) reports a heavy loss in many sections of New York in 1891. Halsted (1893–1901) reports the disease as common from 1892 to 1897, after which it was an unimportant factor in his experiments. Whetzel (1908:436) reports the disease as widespread in New York in 1906. Then followed five years during which the loss in most sections of the State was negligible. Late in the season of 1911, the disease was observed or reported from many fields, and in 1912 it was again severe. The following year there was very little anthracnose to be found except in restricted areas, but it was present to a destructive degree in 1914 and 1915, the loss during the latter year ranging from 30 to 100 per cent of the crop except in a few cases where resistant varieties were grown. During 1916 the damage done in this State was slight, but the disease appeared again from 1917 to 1919, the losses in these years, however, being much less than in earlier years.

A study of the table given in the Plant Disease Survey bulletin (page 254 of the reference already cited) shows that bean anthracnose was generally severe in the eastern United States from 1906 to 1908, from 1914 to 1915, and again in 1917. Individual reports of its severity are recorded in other years. In Maine and New Hampshire it is reported as causing considerable loss nearly every year, while in Western States it rarely does any damage although it may be present.

Figures are not obtainable to show the exact loss from this disease, but in epiphytotic years it is very large, amounting in individual cases to 100 per cent. Muncie (1917:7) estimates a loss in Michigan of $1,500,000 in 1914 and of about $3,000,000 in 1915, while the loss in New York in 1915 probably amounted to $700,000 or more. The Plant Disease Survey

bulletin (page 13 of reference cited) gives the loss during 1917 for New York as 5 per cent, or 83,000 bushels, and for the United States as 1.76 per cent, or 363,000 bushels.

The losses from bean anthracnose are due to poor germination of affected seed, to destruction of affected seedlings, to low yield of affected plants, and to decreased value of the product. The principal loss in the production of green beans is due to the spotting of the pods, which renders them unsalable as snap beans and unfit for canning. Southern-grown beans, apparently healthy when shipped, frequently reach northern markets in a badly spotted condition, and if the disease is common in the field, pods kept over night after picking are likely to be rusted the next morning. The lesion may extend through the pod to the seed, discoloring it. The value of dry seed thus affected is lessened, and the buyer usually deducts a certain percentage, the "pick," from the total weight to allow for this depreciation. A poor stand often results from the planting of spotted seeds, many of which fail to germinate, and this result is augmented by the destruction of seedlings subsequently affected. Plants that have survived the early attack may give an inferior yield due to interrupted growth, although the pods themselves may not become spotted.

SYMPTOMATIC ASPECTS

While the appearance of anthracnose on the various parts of the bean plant has been described accurately by several investigators, a description is included here of its appearance as observed on different varieties of beans under different conditions and at different stages of maturity.

On the seed

The seed of the bean may be discolored by anthracnose, blight, rhizoctoniose, and brown rot, and by various mold-producing fungi. The appearance most characteristic of anthracnose (Plate IV) is the decided blackening of the affected parts. Usually the blackened area has a tawny brown or tan-colored[2] border, or the entire diseased area may consist of the latter color. Specimens are common in which the color of the spot on the seed is lighter, varying from drab to snuff brown or saccardo umber. The larger spots usually have a vinaceous buff to avellaneous-colored,

[2] The colors as given correspond to those given in Ridgway's *Color Standards and Nomenclature*, and, while characteristic, there is considerable variation from them.

often raised, center, which sometimes splits open disclosing the affected cotyledon. The spots may occur on any part of the seed coat, and may appear as a small black or brown speck or involve more than half the surface. In badly diseased seeds the lesion extends through the cotyledon and may even affect the embryo, but in many cases the cotyledon is but slightly or not at all discolored.

On the seedlings

Seedlings from badly diseased seed show blackened cankers on the cotyledons (fig. 10), in which, under moist conditions, small flesh-colored masses appear scattered over the surface of the lesions. The stem may become affected along its entire length, but usually it is affected only below the point of the attachment of the cotyledons. The first indication of a lesion is the appearance of brown specks in the epidermis. Later there appears a browning of the tissues lengthwise of the stem and below the epidermis. Still later, small pits appear along the affected area. Occasionally these cankers become so deep or so numerous that the stem is unable to support the parts above.

On the leaves

The leaves (figs. 10 and 11) not infrequently become badly affected. The lesions appear on the veins, usually on the underside of the leaf. These lesions have practically the same appearance as those on the stem. The tissues on each side of an infected vein and beyond it may wither and die. A considerable area of a leaf may become affected in this manner, giving it somewhat the appearance of blight. Usually only a small part of the leaf tissue is killed, and such places appear on the upper side as angular, elongated, dead areas, which sometimes become torn, giving the leaf a ragged appearance. The petiole may become so badly affected that it cannot support the leaf blade.

On the roots and other parts

The roots of plants growing in the soil are rarely if ever affected; but on seeds sprouted in a moist chamber, where the young roots are exposed, lesions similar to those on the stem may be produced by artificial inoculation. Muncie (1914: 4) mentions a rotting of the root due primarily to the anthracnose and blight organisms followed by secondary rot-producers

FIG. 10. ANTHRACNOSE ON YOUNG BEAN PLANT SHOWING LESIONS ON JUVENILE LEAVES AND ON STEM
(Photographed by H. H. Whetzel)

FIG. 11. ANTHRACNOSE ON BEAN LEAVES

Lesions on the veins cause death of the mesophyll about them, and show as brown dead spots or irregular areas on the upper surface of the leaves

The other parts of older plants may become diseased, and lesions similar to those already described may appear on the branches of the plant and on the pedicels, the sepals, and the bracts of the inflorescence. These parts of plants grown out-of-doors, however, become affected only during protracted periods of weather favorable for the organism.

On the pods

It is on the pods that the disease assumes its most striking appearance (Plate V). The first evidence of it there is the occurrence of tiny brown specks in the epidermis. These may be rufous or ferruginous, slightly elongated areas extending at an angle to the long axis of the pod. These specks enlarge to spots which become black at the center, with a vinaceous-rufous to hazel-colored border of varying width. These

black spots with colored borders are characteristic of anthracnose. The cankers range in size from a mere speck to spots one centimeter in diameter or even larger. By the union of several large cankers, a broad lesion is often formed which may extend from one end of the pod to the other. A canker may extend through the endocarp and even to the seed, particularly if infection takes place early, in which case the pod sometimes fails to develop and becomes shriveled and dried. Cankers resulting from infections that occurred during the later growth of the pod seldom extend below the endocarp. As the pod matures, the lesion is marked at the edge of a canker by a slightly raised, black ring with a cinnamon-rufous to chestnut-colored border. The center of the spot is then somewhat light buff in color. Flesh-colored spore masses on the surface of a young canker dry down to gray, brown, or even black granulations or to small pimples.

The appearance of the disease on the pods of the different varieties is very similar. The lesions on Blue Pod Butter, a variety producing dark blue-purple pods, are snuff brown instead of black in color; otherwise they are similar to those on other varieties. On a number of picked pods that had been left in a basket and were somewhat wilted, and in other cases in which inoculations were made, lesions one centimeter or more in diameter appeared which were light brown in color and marked by a slight depression. If the spores had not been present one would hardly have believed the lesions to be anthracnose, particularly as the typical lesions were present also on some of the pods. In some instances these unusual-appearing lesions later assumed the more characteristic appearance. Lochhead (1903) mentions the presence of a pink rot (*Cephalothecium roseum*) in anthracnose spots on bean pods, and at Ithaca this fungus has been found often in such lesions.

Blight lesions (Plate VI) on the pods may sometimes be confused with anthracnose. The blight lesion consists of an area having a water-soaked appearance extending along the dorsal suture, or of spots of a similar nature and of various diameters appearing on the sides of a pod. Often a pod may have many such discolored spots, these having originated from insect bites or punctures. The spots usually have an ochraceous-tawny center with a border of a cinnamon-rufous color, and commonly, as the pod matures, the entire lesion turns to hazel or to cinnamon brown with a more highly-colored margin. It may be distinguished from anthracnose by the absence of any dark color,[3] by the shape of the lesions which

[3] A saprophytic Alternaria may occur on blighted leaves and pods and give a blackened color to the lesion.

are usually more extensive and more irregular in outline than those of anthracnose, and by the absence of spore masses.

Rhizoctonia (Plate VII) often occurs on the pod, producing lesions which, particularly when they are small, closely resemble anthracnose. This fungus attacks only the pods lying in contact with the ground. The lesion has a bay to auburn center, often with a dark-colored ring near the margin surrounded by a ferruginous border. The lesions are more extensive than those of anthracnose, however, and do not contain the characteristic spore masses (Plate I).

Sclerotinia libertiana Fuckel produces a disease characterized by a soft brown rot and moldy appearance of the pod, followed by a shriveling and drying, which can never be confused with anthracnose. This fungus commonly produces rather large black sclerotia on the pods.

On pods of certain varieties, rust (Plate VIII) sometimes occurs as pustules containing a black mass of dusty spores.

When immature pods are exposed to the hot sun — as is often the case when the leaves are injured by blight or by other means, especially when the plants are approaching maturity — the exposed surfaces become discolored with brown specks, spots, or blotches, in some cases a little sunken, which may be mistaken for blight but hardly for anthracnose. MacMillan (1918) describes these lesions as he found them on certain varieties of beans in Colorado and in the East, and the writer has observed them commonly in the East on many varieties. A peculiar browning, different from sun-scald, was also observed, but the cause was not determined. A browning of pods may occur from other causes also, none of which, however, need be mistaken for anthracnose.

ETIOLOGIC ASPECTS

Name, classification, and synonymy of the causal organism

Bean anthracnose is known to be caused by the fungous parasite *Colletotrichum lindemuthianum* (Sacc. & Magn.) Bri. & Cav., one of the Melanconiales of the classification of Lindau (1900) as used in Engler and Prantl's *Die natürliche Pflanzenfamilien*. The fungus does not differ appreciably in its morphological characters from a number of other species belonging to this genus, nor, except for the presence of setae, from the genus Gloeosporium. Not only are species of the genus Colletotrichum

and of the related genus Gloeosporium similar in appearance, but also the diseases produced by species of the two genera are similar in character.

Saccardo (1878), in his description of the fungus, gave it the name *Gloeosporium lindemuthianum* Sacc. & Magn. after Lindemuth, who discovered the fungus in 1875. Scribner (1888:364) described the presence of setae in the acervuli which were present on most specimens sent him from several States, and thought it probable that the generic name of the fungus should be changed to *Colletotrichum*. The following year Briosi and Cavara (1889) named the fungus *Colletotrichum lindemuthianum* (Sacc. & Magn.) Bri. & Cav., and distributed it as such. The same year Scribner (1889), again finding setae in the acervuli, placed the fungus in the genus Colletotrichum and published it as *Colletotrichum lindemuthianum* (Sacc. & Magn.) Scribner. The name given by Briosi and Cavara stands, although it is evident from much subsequent cultural work that the presence or absence of setae is not a character of sufficient stability to serve as a basis for the determination of generic position. Krüger (1913:294–303) was able to develop setose and non-setose cultures of this fungus at will, finding that a number of factors, such as age of the culture, and nature and moisture content of the substratum, were controlling agencies. He, however, designates the conidial form as *Gloeosporium* (subgenus *Colletotrichum*) *lindemuthianum* Sacc. & Magn.

Halsted (1893d), after making cross-inoculations on bean and watermelon, decided that the anthracnose fungi in these two hosts were the same, and used the name *Colletotrichum lagernarium* (Pass.) Ellis & Halsted, including in the synonymy the names that had been applied to the organism causing melon anthracnose and bean anthracnose, respectively. Shear and Wood (1913:46) found perithecia producing asci and ascospores in cultures made from an anthracnose spot on a bean pod, and they refer their fungus to *Glomerella lindemuthianum* Shear n. comb. Krüger (1913: 311), although he did not find perithecia, designates the fungus as *Glomerella lindemuthianum* Shear n. comb. Edgerton (1915:255–256) questions whether any perithecial stage of this fungus has ever been seen, and suggests that Shear and Wood might have been working with one of the saprophytic forms occurring commonly on bean pods. He believes the fungus should be considered as a species of Colletotrichum until further evidence supports a different view.

At various times other names have appeared in the synonymy of this fungus. Richon (1889) gives the name *Glaeosporium phaseoli* n. sp. to a fungus which he found on the pods and stems of beans at St. Amand, France. His meager description fits this fungus very well, and it is not improbable that he had before him the fungus causing bean anthracnose. Saccardo (1892) lists *Gloeosporium phaseoli* Rich. and gives Richon's description. Allescher (1903) also lists Richon's fungus and gives his description, but says that it is an uncertain species perhaps identical with *G. lindemuthianum* Sacc. & Magn. or with a Colletotrichum.

Allescher (1903) designates as *Gloeosporium lindemuthianum* Sacc. & Magn. forma *foliicolum* Allesch. the fungus he found on the upper surface of subcircular, brownish spots on leaves of *Phaseolus vulgaris* var. *nanus*. An examination made of type specimen No. 380 Allescher & Schnabl (1894), in the herbarium of the Pathological Collection of the United States Department of Agriculture, showed spots somewhat larger and more nearly circular than is usual for anthracnose but not sufficiently distinct to warrant the placing of the fungus as a form of the species. The spores are like those of *Colletotrichum lindemuthianum*. Allescher says the form *foliicolum* is similar to the type except in the appearance of the spots as described and in the absence of setae.

Desmazières (1843a) describes as *Septoria leguminum* Nob. a fungus on the pods of Phaseolus. He ascribes to variety "*b*" of the same species a form on Pisum. Saccardo (1878) says he is not able to decide whether or not *Septoria leguminum* Dsmz. should stand, as he cannot distinguish the young condition from *Gloeosporium lindemuthianum*, but the description varies widely from Septoria and approaches more nearly that of *G. fructigenum* Berk. Berkeley (1881), speaking of dried specimens distributed by Desmazières under the name *Septoria leguminum*, says the species shown is not a good representative of the genus Septoria, but belongs rather to Gloeosporium and has been figured by Saccardo in his *Fungi Italici* as *Gloeosporium lindemuthianum*. Cooke (1881), on the basis of Berkeley's observations, cites *Septoria leguminum* Desm. as synonymous with *Gloeosporium lindemuthianum* Sacc. Kirchner (1906: 137) ascribes to it the small, dry, sharply differentiated brown spots on beans, on which appear later very small black pimples.

Specimens of bean pods distributed by Desmazières (1843 b) as *Septoria leguminum*, deposited in the cryptogamic herbarium of the New

York Botanical Garden, show the presence of the fructifications of two fungi on one of the two pieces of pods in the packet. One of these, occurring in characteristic young anthracnose spots, has the typical spores of *Colletotrichum lindemuthianum* except that the average width, 5.75 μ, is a trifle greater. There can be no doubt that it is the bean anthracnose fungus. The other fungus appears on the specimen as numerous small black pycnidia and these contain typical Septoria spores. The other specimen shows only the Septoria-like fungus. Desmazière's description of the fungus given in *Annales des Sciences Naturelles* (1843 a), and also accompanying the specimen, is of the Septoria, but his description of the disease applies, at least in part, to the condition produced by the Colletotrichum. This probably led to the mistake of ascribing to *Septoria leguminum* Desm. the anthracnose present on pods of *Phaseolus vulgaris* distributed by Von Thümen (1882) as *S. leguminum* and by Roumeguère (1884) as *S. leguminum* Desm. var. *Phaseolarum.* Saccardo (1896) describes a fungus, which he names *Gloeosporium socium* Sacc., as occurring on the leaves of living bean plants (*Phaseolus vulgaris*). But from his description it seems improbable that he has the bean anthracnose fungus. D. Saccardo (1904) labeled as *Colletotrichum lindemuthianum* (Sacc. et Magn.) Cavara f. *brachysporum* specimens of a fungus on bean pod, *Phaseolus vulgaris*, the conidia and basidia of which were recorded as considerably shorter than the normal average. An examination of type specimens in the herbarium of the New York Botanical Garden shows small but typical anthracnose spots, from which, however, no spores were obtained.

Heald and Wolf (1911) have ascribed to a new species, *Colletotrichum caulicolum*, a destructive canker which they found on the stem of Kentucky Wonder beans in Texas. They say that this fungus differs from *C. lindemuthianum* in that the setae are produced abundantly in the host and that the spores are larger and are falcate. Their description of the disease and of the fungus is similar in most respects to that of bean anthracnose and its pathogene, but it is not possible from the description to decide that the fungi are the same. Cooke and Harkness (1880) report *Gloeosporium leguminis* C. & HK. on legumes in California, and later (1884) on pods of Robinia at Sacramento, California. Cooke (1880) describes *Discella leguminum* Cooke on the pods of Prosopis found in Texas. Comes (1891) lists *Discella leguminum* Cooke and *Gloeosporium leguminis* C. &

Hark. as synonyms of *Gloeosporium* (*Colletotrichum*) *Lindemuthianum* Sacc. & Magn. An examination of type specimens of these two fungi in the possession of Dr. C. L. Shear, of the United States Department of Agriculture, leads to the conclusion that they are not at all related to the fungus here considered.

The synonymy would, then, appear as follows:

Gloeosporium Lindemuthianum Sacc. & Magn. Michelia 1:129. 1878.
Septoria leguminum Desm. *In* Von Thümen, Mycotheca universalis, no. 2096. 1882.
Septoria Leguminum Desm. var. *Phaseolarum*. *In* Roumeguère, Fungi gallici exsiccati, no. 2791. 1884.
Colletotrichum lindemuthianum (Sacc. & Magn.) Bri. & Cav. I funghi parassiti delle piante coltivate od utili, no. 50. 1889.
Colletotrichum lindemuthianum (Sacc. & Magn.) Scribner. Orchard and garden 11:193–194. 1889.
? *Glaeosporium phaseoli* Ch. Rich. Cat. raison. champ. Départ. Marne, p. 401. 1889.
Colletotrichum lagernarium (Pass.) Ellis & Halsted. Bul. Torrey Bot. Club 20:246–250. 1893.
Gloeosporium Lindemuthianum Sacc. & Magn. forma *foliicolum* Allesch. *In* Allescher and Schnabl, Fungi bavarici exsiccati, no. 380. 1894.
Colletotrichum Lindemuthianum (Sacc. et Magn.) Cavara f. *brachysporum*. Mycotheca italici, no. 1364. 1904.
Glomerella lindemuthianum Shear n. comb. *In* Krüger, K. biol. Anst. Land- u. Forstw., Arb. 9:311. 1913.

Morphology and physiology

Spores

Whether the fungus is grown on its host or in culture media, the spores are produced abundantly on the surface in acervuli masses of a grenadine pink color. Frank (1883 b:513) mentions the presence of a slimy substance with the spores in the acervulus, and this has since been noted by other workers as a gelatinous substance in which the spores are embedded. If such a mass of spores is placed in water, they separate and become suspended in the water so that they are readily disseminated by its dispersal. If the acervulus remains dry, it hardens and shrinks down to small gray or brown granulations, and the spores are seldom set free under such circumstances.

The summer spores (conidia) are oval or oblong, cylindrical, one-celled bodies of somewhat variable size (Plate III, 1). They are straight or slightly curved, with the ends rounded or at one end somewhat pointed. The dimensions, as averaged from a large number of spore measurements, are 15 by 5 μ. The largest spore encountered measured 22 by 5.33 μ and the smallest 13 by 4.44 μ. The content of young spores is homo-

geneous and granular. Often there is a clear body resembling a vacuole near the center, which Edgerton (1910:20) describes as a nucleus but which earlier workers have regarded merely as a vacuole. Edgerton says that as the spore ages it becomes vacuolate, and finally the contents collect in small masses. The spores are no longer viable when this last stage is reached.

Spore germination

In making germination tests, spores from young acervuli produced in bean-pod cultures were transferred to a drop of the culture medium placed on a flamed slide. The slides were transferred to sterile moist chambers or petri dishes kept moist with wet blotting-paper, in which they rested on glass supports to hold them up from the bottom. The temperature was maintained at about 20° C.

Germination usually takes place by the protrusion of a germ tube from the side of the spore near one end and at an angle to its long axis. On nutrient media some spores have germinated within eight or nine hours (Plate III, 2). Bean agar gives the quickest and largest percentage of germination, although nutrient beef agar, potato agar, and beef bouillon give nearly similar results. Soon after the protrusion of the first tube, a second may be sent out from a similar point at the other end. As many as four germ tubes have been observed coming from a single spore, but rarely are there more than two. Dey (1919:307) observed in a few cases more than two germ tubes developing from a spore. The germ tubes form branches which radiate from it in all directions (Plate III, 4).

Germination takes place more slowly in water than in agar. A few spores were observed to have germinated in water after eighteen hours (Plate III, 10). In certain rain-water cultures about one-half of the spores germinated in twenty-four hours, but this was a greater proportion than the average. In distilled water, germination proceeded somewhat more slowly. The majority of the spores in these water cultures became uniseptate during germination, but septation was not observed to occur so commonly in spores germinating in nutrient solutions. Often there is a constriction of the spore at the septum. In some cases the spores themselves increased somewhat in size before or during germination, but this was not general and when spores were placed in nutrient solutions

it did not occur to any extent. Atkinson (1895) says that septation occurs unless the spore is very short, and that the spore becomes constricted at the point of septation soon after germination. He observed an increase in the size of the spores after germination until they became several times larger than at first, and states that even with spores which fail at first to germinate a similar increase in size takes place, and they become uniseptate, strongly constricted at the septum, and richly charged with highly refringent granules. Edgerton (1910:19) states that the spores swell but slightly or not at all in germinating in nutrient media if they are scattering, but if they are abundant and close together in the culture medium they swell to two or three times normal size in some cases. During the process of enlargement a septum is formed, and with further swelling a constriction of the spore appears at this point. Edgerton finds that "when there are more than 12 or 15 spores to the cubic millimeter of medium, the spores become swollen, germinate slowly and but poorly. When the number is less than this, they germinate with but little, if any, swelling" (page 20 of reference cited). He thinks this may be due to an enzyme prohibiting growth, given off by the spore during germination. Dey (1919) observed that if the drop of water used in the culture had a convex surface, the spores lying in the middle hardly germinated while most of those at the border did. He thinks this difference is due to a difference in the oxygen supply.

The germination of the spore in water consists, in most cases, of the production of an appressorium at one or both ends of the conidium (Plate III). This is a subglobose body flattened on one side, having dark-colored, thick walls and containing dense granular protoplasm. It often appears attached directly to the conidium or is produced at the end of a short germ tube, although it is not uncommon to find an appressorium at the end of a long, narrow hypha. In the ordinary process of germination in nutrient media, the spore contents become coarsely granular and the vacuole increases greatly in size or there may be several vacuoles. In rain-water cultures, the spore contents during germination seem to pass into the appressorium, in which the protoplasm appears to be very dense.

The appressoria in most cases are closely appressed to the slide. A few have been noticed, however, which were apparently free, as they were observed to move when the slide was jarred. In the course of twenty-four

hours some of these appressoria themselves send out a slender germ tube, at the end of which in most cases another appressorium is formed. After nine days about 50 per cent of the spores in this experiment had germinated but had not proceeded much beyond the production of appressoria. A number of spores had the appearance of being empty, and other peculiarities were noticed to which no importance could be attached.

Frank (1883b:513–515) describes the germination of the spore and the formation of appressoria, he being the first to apply the name to these bodies. These appressoria, Frank says, come to have a thick, irregular, dark purple membrane. They are produced abundantly when spores are germinated on the surface of bean or cucumber tissue, but seldom occur when germination takes place in water on a glass plate. Instead, long, thin, germ tubes are formed, at the end of which a small appressorium may appear, or the spore may produce another spore or sporidium attached directly to the spore or to a short tube. Frank says the appressoria do not germinate unless they are in contact with the host. He thinks their production is stimulated by the quality of the substratum, and suggests that their function is to prepare the fungus for penetration into its host plant.

Appressoria are produced by other Gloeosporia of the Glomerella type, and their significance has been discussed by other writers. Halsted (1893a:305) suggests that they may be formed as a protective body to tide the germinating spore over unfavorable periods. He says that, while the appressorium is often a single cell, it may become an aggregation of thick-walled cells like a sclerotium. He thinks the appressoria may be of taxonomic value. Stoneman (1898:113) does not find them to occur as a constant character, but thinks they may be forced in certain species by lack of nourishment. Hasselbring (1906:142), from studies of *Gloeosporium fructigenum* Berk., believes them to be adhesion organs during early stages of infection, and thinks they are formed as a result of contact stimuli of the germ tube but lose this power of reacting in nutrient media. He calls attention to the presence of a germ pore in the flattened side, through which the germ tube protrudes during germination. He finds the appressoria much more resistant to desiccation than the spores. Edgerton (1910:21) finds appressoria produced in nutrient media, often not in contact with the glass or any solid substance; and in this species, *Colletotrichum lindemuthianum*, the "germ pore" is often lacking.

Gardner (1918:21), in his spore-germination studies of *Colletotrichum lagenarium*, concludes that a rather abundant supply of oxygen and a contact stimulus is necessary for appressorium formation, and that the presence of food material does not seem to inhibit such formation. Dey (1919), in his studies of *C. lindemuthianum*, states that appressoria are formed whenever the germ tube comes into contact with a hard foreign substance which acts as a stimulus for their formation. He found no germ pore in the appressoria observed, but noted that the germ tube arose from the side in contact with the glass. He observed the appressorium to be sheathed in a mucilaginous coat, which aids it in becoming attached to a foreign substance so firmly that even a jet of water fails to dislodge it.

In all the cultures made in fresh nutrient media, the germination was rapid, the germ tubes were as large, or nearly so, as the spores, few or no appressoria were formed, and the subsequent development of the mycelium was luxuriant; while in water cultures, the germination was slow, the germ tubes were much smaller in diameter, the production of appressoria was abundant, and subsequent development of mycelium was scanty or there was none at all. It is true that appressoria were commonly produced in nutrient media that was becoming somewhat dry and hard, as occurred soon when only a little was poured into a petri dish. When a nutrient medium is poured over a water culture, as suggested by Hasselbring (1906), the appressoria germinate within a few hours and produce a rich mycelial growth.

Mycelium and spore production in culture

Under favorable conditions for growth, the germ tube branches to form hyphae, and these in turn, by further growth and branching, develop within forty-eight hours into a mycelial mat often one millimeter in diameter. In three or four days conidia are produced at the ends of the hyphal threads. In several agar cultures in this experiment they were produced abundantly on short threads within twenty-four hours. They are formed by the constriction of the wall near the extremity of the hypha. A spore thus formed is pushed aside and the hypha elongates to about the same point, when constriction again occurs. In this way several spores are formed from a single branch, and can be seen lying side by side or piled in a heap at the end of the branch (Plate III, 5). Atkinson (1895:309) observed conidia being produced directly on the

spore, and in the writer's cultures this condition was frequently met. Atkinson found that the ends of the hyphal threads have a dichotomous appearance, due to a branch just behind the growing end overtaking the primary thread, and that a plumose tuft is produced by this dichotomous branching taking place successively in the same thread.

The mycelium, which at first is white, will become dark-colored after a growth of several days in a starch-containing medium. This is especially noticeable with the growth in potato agar and bean agar and on sterilized bean pods. A culture four or five days old shows a dark center with pure white mycelial growth at the margin and aërial mycelium developing over the surface. As growth continues, dark-colored knots of mycelial threads appear scattered from the center outward, and above these darker parts of the culture, flesh-colored masses of spores (acervuli) begin to be produced if the culture is in good condition. Dey (1919) finds that in cornmeal agar cultures these spores are surrounded by small dark spines. On sterilized bean pods inoculated with spores kept at a temperature of about 22° C., there is a rapid growth of mycelium which in two days begins to darken and after three days produces spores in acervuli. In six days the pod is covered with a pale salmon or pale flesh-colored mass of spores. Cultures kept for a long time or at unfavorably high temperatures lose their power to develop spores in this way when transferred to fresh media. Commonly they develop only a slow growth of white mycelium. Spores will usually be produced if the mycelium turns dark.

Viala and Pacottet (1905), from a study of *Colletotrichum lindemuthianum* in culture, report the production of spermagonia, pycnidia, cysts, yeasts, and sclerotia, as well as conidiophores, similar in most respects to those produced by *Manginia ampelina*, another fungus under their observation. Shear and Wood (1913:64) say yeasts have never occurred in their cultures of Gloeosporia except where they were evidently contaminations, and they have never observed the production of spermagonia or pycnidia by these fungi. No other writers in speaking of *C. lindemuthianum* or related forms have mentioned the production of bodies of these kinds, except that Edgerton (1910:10) reports having once found pycnidia-like bodies in the tissue of the bean seed.

Temperature is an important factor in the development of the fungus in connection with its host or in culture media. Edgerton (1910:29)

found that the fungus died in culture at Baton Rouge, Louisiana, during the summer, even when frequently transferred to fresh media, and later (1915) showed that the temperature requirements for this fungus are lower than for other anthracnose fungi, the optimum being about 22° to 23° C. though there is but little difference in growth between 19° and 26°. Edgerton gives the maximum as about 30° or 31° C. The growth at optimum temperatures is between 3 and 4 millimeters a day. Muncie (1917:9–11), after subjecting test-tube cultures of old mycelium to a water bath at 65° C. for ten minutes, found that good growth could yet be obtained but that the thermal death point of young mycelium lies between 50° and 52.5° C. and that of spores between 45° and 48° C.

The writer endeavored to determine the minimum, optimum, and maximum temperatures for growth and production of spores. Potato agar plate cultures of two physiologically different strains of *Colletotrichum lindemuthianum* were kept for a few days at 25° C., after which blocks of agar 3 millimeters in diameter of each strain were transferred to plates of potato agar and corn agar and to tubes of sterilized bean pods. The temperatures (centigrade) at which the cultures were placed were, respectively, 0°, 4°, 10°, 16°, 22°, 28°, 34°, 40°, 43°. Two cultures of each strain in potato agar and two of each in corn agar were placed at each of these temperatures on April 8, 1914. The growth made by them is shown graphically in figure 12.

It is seen that the average growth during the first six days was less than on the eight succeeding days at the temperatures 4° and 10° C., but was greater at temperatures above 28° C. Growth was probably checked during the first day or two at the lower temperatures by an abrupt transfer from a warm room, but was resumed to some extent later. While the growth was no doubt checked by the transfer to the higher temperatures, and ceased altogether after a few days at 34° and above, yet some growth was possible during the first day or two because the temperatures then ranged between room temperature, at which the cultures were started, and the higher temperatures. The figures giving the average growth on the eight days following the first six represent more nearly accurately the actual growth that occurs at these temperatures under these conditions. Considering, then, the curve representing such growth, it appears that the minimum temperature for growth lies at 0°, the optimum at 22°, and the maximum at 34°. As a matter of fact, the

minimum lies somewhere between 0° and 4° C., the optimum near 22°, and the maximum between 34° and a few degrees lower. This corresponds very closely to the observations of Edgerton (1915:254). The corn agar permitted a little better growth than the potato agar.

The growth at 4° C. was white, with considerable aërial mycelium in most cultures. After four weeks a growth of from 25 to 35 millimeters

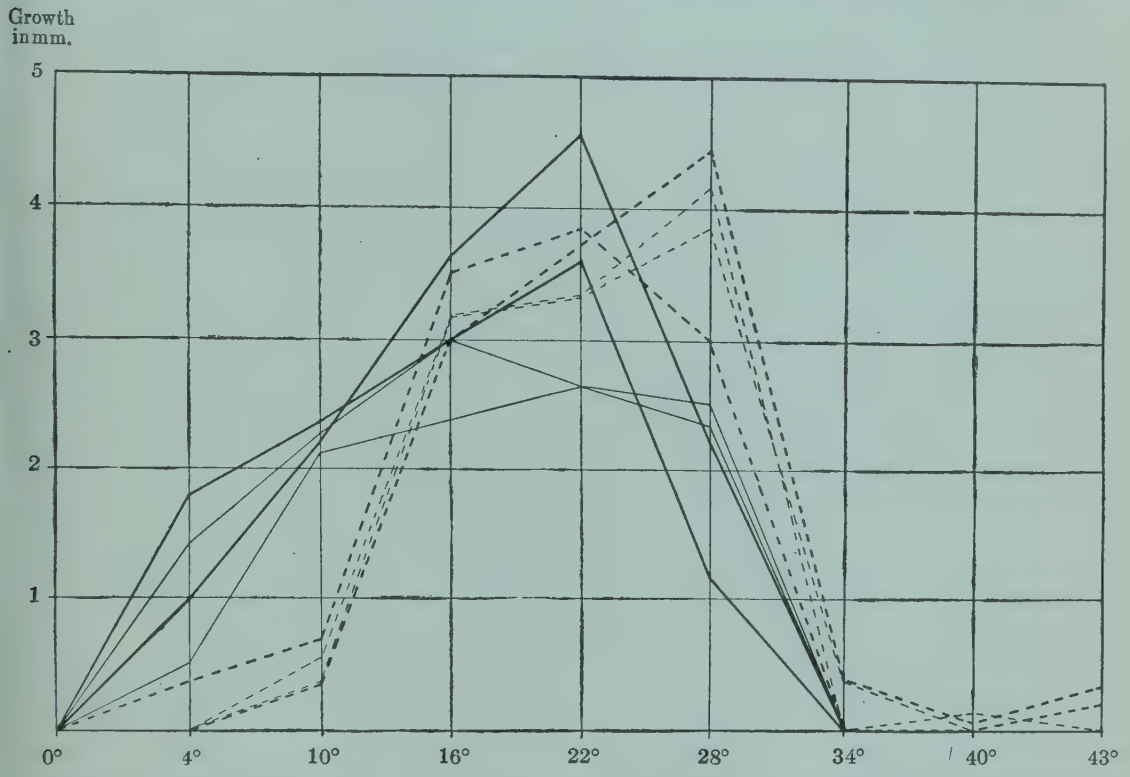

FIG. 12. CURVE OF GROWTH OF TWO STRAINS, A AND B, OF COLLETOTRICHUM LINDEMUTHIANUM AT VARYING TEMPERATURES

The light curves represent growth in potato agar, the heavy curves growth in corn agar. The dotted lines represent average growth per day during the first six days; the straight lines, average growth per day during the following eight days. The temperature is expressed in degrees centigrade

was attained, and an olivaceous color, with spore production, was noticed in a few agar and bean-pod cultures. Spores were produced in abundance on bean pods at 10°, 16°, and 22° in six days, and but sparingly at 28°. As already stated (page 121), bean pod cultures kept at 22° C. have been found to give a rapid and abundant production of spores when the fungus was in a spore-producing condition, in hundreds of cultures made by the writer.

The relation of growth of this fungus to acid and alkaline media has not been studied by the writer, though he has observed that not as good growth is secured when the fungus is cultured in a potato-agar medium made acid by the addition of one drop of 50-per-cent lactic acid to 10 cubic centimeters of medium, as when such acid is not added. Edgerton (1910:28) records a fair growth of *Colletotrichum lindemuthianum* at −16 Fuller's scale, excellent growth at +5, and only slight growth at +20. *Glomerella gossypii* (South.) Edg. grew better than did *Colletotrichum lindemuthianum* in the more acid media.

The ascogenous stage

The ascogenous stage of many anthracnoses has already been found in nature or produced in culture. Klebahn (1905) has shown that the Gloeosporium causing sycamore anthracnose is a Gnomonia. He also (1907:65) found the perfect stage of *Gloeosporium ribes* (Lib.) M. & D., causing an anthracnose of currant leaves, to be a Pseudopeziza. Burkholder (1917:164) discovered the perfect stage of *Gloeosporium venetum* Speg. on raspberries to be a Plectodiscella, which he named *P. veneta* Burkholder. Genera representing perfect stages of other Gloeosporia that have been reported (Stevens, 1913) are Glomerella, Gnomoniella, Gnomonia, Trochila, Physalospora, and Calospora. Most of the anthracnose fungi parasitic on fruits and herbaceous plants, including the one on bean, belong to what is known as the Glomerella type, that is, their perfect stage when found is of the type of the genus Glomerella. Even in their imperfect stage they differ somewhat from the other forms. Edgerton (1908:384) has pointed out the following important differences, among others of minor importance:

Glomerella type	Gnomonia and Pseudopeziza types
Spores oozing out as a pink mass	Spore mass white, cream-colored, or yellow
Appressoria produced in certain cultures under certain conditions	No appressoria observed
Mycelium in culture varying but little in diameter	Mycelium in culture varying in diameter (at least in Gnomonia type)

Stoneman (1898:99–112) was the first to discover the ascogenous stage of a Gloeosporium of the Glomerella type, and she described five species occurring in nature or in culture. These were placed in a new genus of the Gnomoniaceae which Stoneman named Gnomoniopsis. Since then the perfect stages of at least thirty-two other Gloeosporia or Colletotricha have been found in nature or produced in culture. Von Schrenk and Spaulding (1903), because of a prior use of the name Gnomoniopsis, substituted for it the name Glomerella.

Shear and Wood (1907, a and b, and 1909) have produced in culture the perfect stage of anthracnose fungi from a large number of hosts, and among them what they believed to be the ascigerous perithecia of *Colletotrichum lindemuthianum*. They say that light, temperature, and moisture are not factors of much importance in producing this stage. They hold that once a race, a strain, or a generation is obtained that will produce the perithecia, these may be produced in various media and under diverse conditions. Moreover, they state that if a given strain will not produce perithecia in sterilized cornmeal at 75° to 85° F., it is useless to try longer to obtain them from that strain. In a later publication (1913:14), after having studied forms on forty-five different hosts and having obtained the ascogenous stage from thirty-six hosts, they refer forms from thirty-nine hosts to *Glomerella cingulata* (Stonem.) S. et v. S., the one from cotton to *Glomerella gossypii* Edg., the one from bean to *Glomerella lindemuthianum Shear*, those from watermelon, cucumber, and squash to *Gloeosporium lagenarium* (Pass.) Sacc. & Roum., and the one from banana to *Gloeosporium musarum* Cke. & Mass.

In the same publication (1913:46–47) Shear and Wood record the finding of perithecia producing asci and ascospores in flasks of cornmeal from cultures made from an anthracnose spot on a bean pod. While the perithecia were abundant, conidia were scarce or wanting. Numerous subsequent plate cultures made from crushed perithecia and asci and from single ascospores produced the usual growth of mycelium and abundance of perithecia with mature asci, but no conidia were seen. Shear and Wood believe this form to be an extreme variation of a condition they have noticed in respect to cultures from other hosts, in that cultures from ascospores produce fewer conidia than do cultures made from conidia.

Edgerton (1915:255) thinks it doubtful that any perithecial stage of *Colletotrichum lindemuthianum* has ever been seen, and that Shear

and Wood were not working with a culture of the true bean-anthracnose fungus but rather with one of the saprophytic forms which Edgerton finds occurring commonly on old parts of bean and other plants. These forms produce perithecia abundantly, but no conidia. In hundreds of cultures of *C. lindemuthianum* examined by him, no perithecia have been found, and he thinks that until more satisfactory proof is offered of the presence of perithecia it is better to consider the bean anthracnose fungus as lacking an ascogenous stage.

Relation of fungus to host

Penetration of the host

Frank (1883b:515) described in detail the germination of the spore and the penetration of the host. He says that the spore, on germinating, produces a germ tube, which on coming into contact with the epidermis of the host forms an appressorium closely pressed against the surface of the epidermis. This either remains unchanged, or after a time becomes thinner and colorless on one side, and from this spot a germ tube appears. The germ tube penetrates directly through the cuticle into the epidermal cell, and either fills this cell with branching hyphae or quickly penetrates the adjoining epidermal cells or those beneath. Voglino (1892), from inoculations of parts of green bean pods, observed the germination of the spore, the quick formation of large numbers of appressoria, and the production of mycelial filament which penetrated into the interior of the epidermal cells. Dey (1919) has carefully studied and figured this penetration from stained sections made from material embedded in paraffin. He finds that a peg-like infection hypha grows out from the surface of the appressorium in contact with the host, which mechanically ruptures the cuticular layer and then brings about a swelling and disintegration of the subcuticular layers — probably by enzymic action. The infection hypha was never observed earlier than forty-eight hours after inoculation. The rupture of the cuticle is the result of the pressure exerted by the development of the infection hypha. This hypha is very fine at first, but reaches a normal size while growing in the cellulose layers below the cuticle. Here, or farther on in the cell, it produces a small vesicle from which one or more branches arise and extend into the host tissue. As the invading hypha enters the cell, the protoplasmic contents collect around it, and later a collapse of the cell takes place. The writer has never observed this

penetration. It seems that this is the really critical time in the development of the fungus, for it must overcome the protoplasm of the host cell before it can continue its development. Varieties of beans immune to certain strains of *Colletotrichum lindemuthianum* probably owe this immunity to the inability of the infection hypha of the fungus to overcome the resistance offered it by the protoplasm of the host cell. The writer (Barrus, 1918:594) has shown that some such varieties, on inoculation with such a strain, have shown on their pods and stems a slight but distinct specking, as though the fungus had entered the tissue and killed a few cells but was unable to proceed farther. This specking did not appear on the pods of plants not inoculated.

Once the fungus has established itself within the host cell, the hyphae extend horizontally and diagonally into other cells, penetrating the cell walls of the host as they come into contact with them (Plate II). In some cases the hyphae enlarge when in contact with the cell wall, and a small hole is formed through which projects a slender tube that at once enlarges after passing through. As many as twelve hyphae have been observed penetrating a single cell (Plate II, 4). Growth within the host is rapid, particularly if the tissue is young and tender. The protoplasm of the host cell is killed and turns brown soon after being attacked. The walls collapse, and after from four and one-half to seven days a lesion may be observed on the surface.

There seems to be a great difference of opinion as to the length of the period of incubation. Frank (1883a:33) noticed the beginning of a browning of the epidermis at separate points on the pods twenty-four hours after inoculation was made. This browning had extended by the following day, and five days after inoculation Frank obtained the first spores in the new lesion. Scribner (1888) states that the cells become discolored almost at once after the hyphae enter. Halsted (1892:284) found a spot on an otherwise healthy pod thirty-six hours after inoculating it in the laboratory under the most favorable conditions. Pammel and King (1909) report having obtained an anthracnose spot thirty-six hours after inoculation. Dey (1919) claims that early specking appears on a pod when tap water is substituted for infection drops, and thinks it due to osmotic disturbances. Edgerton (1910:14) finds from inoculations made on plants in the greenhouse and in the field that the period of incubation ranges from four and one-half to nine days, depending on the

weather and on temperature conditions. The writer's numerous observations are in accord with this as regards the production of typical anthracnose lesions. Temperature appears to have some influence on the length of the incubation period; also, the period varies considerably with the different varieties of beans under the same conditions. Schaffnit (1920) finds that the incubation period, and also the period between infection and spore formation, differ with different varieties.

Reproduction of the fungus within the host

At about the time when the cell walls collapse to form a canker, or even earlier in many cases, the mycelium at certain points develops abundantly in the epidermal cells and in those just beneath, forming a stroma of closely crowded, many-septate hyphae. The host cells at these places are so flattened that it is difficult to observe them (Plate II, 2) From this pseudoparenchymatous tissue arise short, more or less erect, conidiophores, from 15 to 20 μ long and from 4 to 5 μ broad, at the apex of each of which is borne a small conidium rounded at the top and drawn out to a point at its attached end. This conidium enlarges somewhat before becoming detached. The conidia are formed by the constriction of the upper end of the conidiophores, as described in connection with germination in culture media. Spore after spore is produced by the conidiophore; the cuticle, which has been pushed up to form black pimples in the canker as the conidiophores elongate, is soon ruptured, and the spores emerge in a gelatinous pink mass (Plate I, 1) Frank (1883b: 513) describes the formation of the stroma and the production of spores enveloped in slime, the rupture of the cuticle, and the behavior of the spores thereafter.

These first acervuli formed at the center are followed by the production of others as the lesion enlarges. In a single lesion there may be fifty or more acervuli, in which thousands of spores are produced. Edgerton (1910: 12) estimated that on a badly spotted pod, from 110,000,000 to 115,000,000 spores had been produced. After washing these off and placing the pods in a moist chamber for twenty-four hours, he found that about 50,000,000 more spores were produced, and he concluded that a total of from 500,000,000 to 1,000,000,000 spores may develop on some pods. If the weather remains moist and cool, the conidiophores will continue to produce conidia; but during dry weather the spore masses harden down over the acervulus and spore formation ceases.

As the acervuli become older, long-pointed, brown, septate hyphae (setae) are produced here and there among the conidiophores and often in a ring near the margin. These range in length from 30 to 90 μ. Some taper evenly to a point from a base 8 to 10 μ wide; others have a bulbous base, which Beach (1892:319) reports as being often many-celled; many do not taper evenly but are swollen near the septa. They vary in number from a few to as many as twenty in an acervulus (Plate I, 2). Black stromata made up of dark-colored hyphae are produced on the surface of dead areas of leaves spotted by anthracnose and on the surface of dry pods, and these invariably support setae. Setae are abundantly formed also in old agar and bean-pod cultures. Frank (1883 b:517) found them in lesions on bean pods, and describes them as sterile, brown, hair-like appendages of the fungus.

The fungus in the seed

The fungus passes the winter in the seed as mycelium lying within the cells in a more or less dormant condition. It may be confined to the cells of the seed coat, but in badly diseased seeds it occurs in the cells of the cotyledon. It exists there as vacuolate, closely septate, hyphae, from 3 to 5 μ in diameter, which are wound about in the cells or extend diagonally across into other cells. It may occasionally be found as a cobwebby growth between the seed coat and the cotyledon, or even between the two cotyledons within the seed. Frank (1883 b:520) found spores produced in lesions of the seed, Scribner (1888) says that spores and basidia may be found between testa and embryo, and Halsted (1892:285) found them borne in the cavity between the cotyledons of the diseased dry seed. Halsted called attention to the rapid growth of the fungus and to the production of spores on the diseased seed when it is placed under a bell jar. Edgerton (1910:10) notes that acervuli are often present on the surface of the spots and between the cotyledons, and finds peculiar closed pycnidia-like bodies buried some distance beneath the surface of the bean.

Gain (1898) has shown that the density of attacked seeds may be lowered as much as 4.7 per cent. Muncie (1917:37) states that badly affected seed will remain on the surface of a solution of sodium nitrate of given concentration, while slightly affected and clean seed will sink in it.

The viability of the seed also is affected according as the mycelium has or has not penetrated beyond the epidermis which protects the embryo. Gain (1898 and 1899) says that 10 per cent of the affected seed planted did not germinate, 8 per cent germinated but did not grow, and 36 per cent, although affected, were viable; while 46 per cent having only the integument but not the cotyledon affected produced healthy plants, as the fungus cannot produce fructifications unless it has penetrated into the cotyledon. Seed affected to one-twentieth of their volume are not viable. Gain says also that the disease can be quickly communicated from one seed to another by contact, or by inoculation with spores. Halsted (1892) states that only half of the diseased seed germinated, and those that did germinate produced plants of a sickly nature. Observations made by various other workers seem to prove that affected seed germinates poorly. The experience of the writer indicates that the percentage of germination of anthracnose-affected seeds is dependent mainly on the tissue affected and the area of the lesion. If the embryo or the tissues near it are affected, the seed usually will not germinate. When conditions are far from optimum for germination of bean seed, affected seeds often do not germinate, but neither will healthy seed germinate well under such conditions. The larger proportion of plants appearing from healthy seed than from affected seed under unfavorable conditions for germination is due to the attack of the new tissues by the anthracnose fungus and sometimes by other fungi associated with it. Edgerton (1910:36) obtained a much lower percentage of germination from anthracnose-spotted seed planted in unsterilized soil than from that planted in soil that had been sterilized, due to rot organisms in the unsterilized soil which attacked such seed. He says, however, that in the latter case the great majority of plants appearing were destroyed by anthracnose, while in the former there was greater freedom from the disease, indicating to him, as did other trials and observations, that rot organisms of the soil, especially a certain Fusarium commonly associated with anthracnose spots on seed after planting, will in Louisiana greatly reduce the severity of the anthracnose.

It appears that when a diseased seed is placed in a fairly moist situation, the threads of the fungus, theretofore dormant, renew their activity, extending into healthy cells beyond and forming spore-bearing conidiophores at the surface of the lesion. These conidiophores appear first as small black pimples in the lesion, from which spores issue in small,

pinkish, pasty masses. As already mentioned, if the acervulus remains dry these spores harden down to little gray or brown granulations, and the spores are seldom set free under such circumstances. Ordinarily the lesion becomes wet with soil moisture or later with rain or dew, and then the spores separate from one another and become suspended in the water. Sometimes the entire seed becomes enveloped by a moldy growth of the fungus and fails to germinate; but when a diseased seed is viable and soil conditions are favorable, spores may be produced in the diseased parts of the cotyledons by the time they have appeared above ground. If the soil is sufficiently moist as the seed is emerging from the ground, spores are set free and these are able to infect the young and tender stems.

Infection of the seedling from affected seed

The plumule, consisting of the young leaves, is during germination and for a short time thereafter in intimate contact with the cotyledons (fig. 13). The water containing the suspended spores, by capillarity and

FIG. 13. SEEDLINGS PHOTOGRAPHED TO ILLUSTRATE MANNER OF INOCULATION OF JUVENILE LEAVES FROM SPORES PRODUCED ON COTYLEDON
Seven-eighths natural size

in other ways comes into contact with the now exposed under surface of these leaves. The stem may also become inoculated with spores that have been washed down from the cankers on the cotyledons, especially the base of the stem just below the surface of the soil, where moisture conditions are favorable for the germination of the spores. Frank (1883b:522) says that after affected cotyledons fall from the growing seedling, the fungus continues to grow in them and produces spores in great abundance which are washed by rain into the soil and bring about an infection of the plant in this way. Spattering of contaminated water and of soil also serves to inoculate the seedling; this is discussed more fully later.

Dipping seed in a suspension of spores just before planting will bring about an infection of the cotyledons and other parts of the seedlings, as has been shown by Edgerton (1910:41) and verified by the writer. Gain (1898) proved that the soil can become contaminated and serve as a source of inoculum.

Seeds planted in soil to which water containing spores of this fungus is applied will also produce infection. On August 22, 1910, thirty-six clean bean seeds were planted in twelve pots and watered with a suspension of spores of *Colletotrichum lindemuthianum*. As a check, six seeds were planted in two pots to which water without spores was applied. On September 6 thirty-one plants had appeared in the twelve pots, of which thirty, or 96.8 per cent, were infected. None of the six plants that appeared in the check pots were affected. On August 30, 1910, fifty clean seeds of the variety Golden Refugee were planted in a flat in clean soil, and water containing spores of *C. lindemuthianum* was poured over the surface until the soil was wet. On September 9 forty-nine plants had appeared, of which six showed anthracnose lesions. No later observations were made.

Longevity of fungus in soil

In order to find out whether spores washed to the soil would remain viable over winter, the following experiment was carried out. On November 27, 1916, twenty-five 8-inch pots were filled with loam and sterilized in the autoclave for three hours at twenty pounds pressure. On December 15, fifty test-tube cultures of *C. lindemuthianum* grown on

sterilized bean pods were placed in 4 liters of tap water and the spores were washed off. The suspension was then filtered through a mat of absorbent cotton to eliminate fragments of plant tissue. Twenty-one pots of soil were inoculated by pouring over the surface of each about an equal portion of the suspension. There being some of the suspension left over from the first application, a double portion was applied to three pots. Four pots did not receive any spores, and these were labeled *Checks.* Several thicknesses of cheesecloth were tied over the top of each pot and the pots were placed outdoors. In the course of the winter and spring, the pots were taken into the greenhouse and planted with Davis White Wax, a susceptible variety, the seed used having come from healthy pods and having been carefully sorted. Twenty-five seeds were planted in each pot. After the beans were planted, unused sphagnum was placed over the surface to the depth of an inch to keep the surface of the soil in a moist condition. At the last trial, on June 8, four of the pots were inoculated again with a fresh suspension of spores as a control. The results are given in table 3. It was thought that the pots planted on

TABLE 3. RESULTS OBTAINED BY GROWING BEANS IN SOIL THAT HAD BEEN INOCULATED WITH A SUSPENSION OF SPORES OF COLLETOTRICHUM LINDEMUTHIANUM, AS COMPARED WITH THOSE GROWN IN UNINOCULATED SOIL

Date of planting	Date of examination	Type of inoculation	Number of plants appearing	Number of plants affected	Remarks
Dec. 15, 1916	Jan. 6, 1917	2 single	25	11	Small lesion at base of stem
			25	2	Ditto
Jan. 30, 1917	Feb. 25	1 double	21	17	Well-defined lesions on stem
		1 single	24	2	Ditto
		1 check	23	0	
April 13	May 7	2 double	25	0	
			24	0	
			24	0	
		3 single	25	0	
			25	0	
		1 check	24	0	
Pots replanted May 7	May 29	2 double	25	4	Well-defined lesions on stem. All 4 affected plants adjoining
			24	0	
			22	0	
		3 single	22	1	1 small lesion on stem
			24	0	
		1 check	24	0	

TABLE 3 (*continued*)

Date of planting	Date of examination	Type of inoculation	Number of plants appearing	Number of plants affected	Remarks
June 8	June 24	8 single	23	0	
			24	1	5 old lesions on stem
			25	0	
			23	0	
			22	3	1 with several old lesions. 2 with new lesions, apparently secondary infection
			25	2	2 with one new lesion, apparently secondary infection
			25	0	
			25	1	4 old lesions
		2 checks, not inoculated	25	0	
			25	0	
		4 recently inoculated	24	24	Stems badly affected
			22	22	Ditto
			22	19	Ditto
			24	17	Ditto

April 13 may not have given infected plants because the surface of the soil had been allowed to remain dry for some time through neglect. As no new spores had been produced to vitiate the experiment, these pots were replanted on May 7.

It would appear from this experiment that a few spores are able to live over winter in the soil outdoors and bring about infection the following spring. It is but fair to say, however, that the plants were not in any case screened from greenhouse insects that were present, and that other inoculation experiments with bean anthracnose were being conducted by other persons in another compartment of the same house and in adjoining houses. This may account for the few cases of disease occurring in the spring experiments. The infection is very light compared with that occurring on plants grown in freshly inoculated soil. Under practical bean-growing conditions the chances of infection from this source must be negligible.

An experiment similar to the one recorded above was tried the following winter, the same methods being employed. A greater effort was made, however, to keep the surface of the soil moist at all times, and also unsterilized but presumably uncontaminated soil, as well as sterilized soil, was used. On January 5, 1918, all the pots were well moistened with tap water, soon after which a suspension of spores was poured over the

surface of the soil of those to be inoculated. Sterilized sphagnum was then placed over the soil to the depth of an inch, and covers were tied over the tops of the pots. After three days some of the pots were placed outdoors, being set in the soil so that the tops were level with the surface of the ground; others were left inside the violet house, where the temperature is kept cool. Check pots not inoculated were similarly prepared. At each planting made thereafter a control pot, made up of fresh uncontaminated soil, was inoculated in the same manner as were the pots inoculated earlier. Twenty-five clean beans of the variety Refugee Wax were planted in each pot except in the first planting, when the variety Extra Early Refugee was used. After planting, the pots were kept in the warm house. The results are given in table 4.

TABLE 4. RESULTS OBTAINED BY PLANTING BEANS AT VARIOUS TIMES IN SOIL INOCULATED WITH A SUSPENSION OF SPORES OF COLLETOTRICHUM LINDEMUTHIANUM, AS COMPARED WITH THOSE GROWN IN UNINOCULATED SOIL

Date of planting	Date of examination	Description of pots used	Number of plants appearing	Number of plants affected	Remarks
Jan. 5, 1918	Jan. 25, 1918	Check (not inoculated):			
		Soil sterilized	25	0	
		Inoculated:			
		Soil not sterilized	22	21	Varying from 2 excellent, to those with a slight lesion at base of stem
Jan. 17	Feb. 17	Check (not inoculated):			
		Pots left outside:			
		Soil sterilized	17	0	
		Inoculated:			
		Pots left outside:			
		Soil sterilized	21	1	Slight lesion on stem
		Soil not sterilized	7	0	
		Pots left inside:			
		Soil sterilized	23	2	Fair halfway up stem
		Soil not sterilized	17	5	One or more lesions on stem
Feb. 20	March 11	Check (not inoculated):			
		Pots left outside:			
		Soil sterilized	21	0	
		Soil not sterilized	13	0	
		Inoculated:			
		Pots left outside:			
		Soil sterilized	20	0	
		Soil not sterilized	15	0	
		Pots left inside:			
		Soil sterilized	20	0	
		Control (fresh soil used):			
		Soil inoculated 2–20–18	19	19	Lesions, many of them large, on stems

TABLE 4 (*continued*)

Date of planting	Date of examination	Description of pots used	Number of plants appearing	Number of plants affected	Remarks
April 3	April 19	Checks (not inoculated):			
		Pots left outside:			
		Soil sterilized.....	24	0	
		Soil sterilized.....	18	0	
		Inoculated:			
		Pots left outside:			
		Soil sterilized.....	22	0	
		Soil sterilized.....	19	0	
		Soil sterilized.....	19	0	
		Soil not sterilized....	25	0	
		Soil not sterilized....	18	0	
		Pots left inside:			
		Soil sterilized.....	24	0	
		Soil sterilized.....	19	0	
		Soil not sterilized....	13	0	
		Control (fresh soil used):			
		Soil inoculated 4–3–18..	16	13	Excellent on stems

It appears fairly evident that spores of *C. lindemuthianum* removed from the acervulus and remaining in the soil for a period of two weeks or more are able to bring about an infection of susceptible bean seedlings grown in such soil, but not after six and one-half weeks. Under field conditions, however, in addition to spores being washed into the soil, there are many bits of plant tissue, some of which would probably be infected tissue, remaining on the soil after the beans are harvested.

Frank (1883 b:521) tested the germination of spores which he found produced in the lesions of dry seed. He concludes that spores attached to the basidium remain viable throughout the winter, while those produced earlier and unattached are unable to survive. Edgerton (1910:25) has studied in a different way the question of the viability of these spores. He finds that the old spores on or within affected seeds are capable of germinating in nutrient media, and suggests the possibility of the infection of seedlings from healthy seeds by such spores, they having been transferred to the healthy seed by contact with affected ones. He finds also that good germination takes place in agar after the spores have remained dried for thirteen days in their mucilaginous matrix or washed free from it, and states that some germination took place after twenty-two days had elapsed.

Infection was also brought about, in an experiment, by placing recently affected vines or pods on or in the soil before the bean plants appeared. On August 8, 1910, vines of the current year badly affected with anthracnose were placed in a flat and covered to the depth of an inch with soil. On the surface of this soil, fifty hand-sorted Refugee Wax bean seeds were planted. These were covered lightly with soil. The soil came from a neighboring field that had not produced beans for years. The flat was then placed outdoors and watered once with well water. All the seeds produced plants, which on August 22 were not affected on any part above ground. On August 29 forty-two plants had appeared, of which thirty-five, or $83\frac{1}{3}$ per cent, showed lesions on stem, on leaves, or on both.

On August 22 one hundred clean Refugee Wax seeds were planted in clean soil in a flat and covered lightly with soil. Over the surface was placed a quantity of immature pods badly spotted with anthracnose and producing spores. On September 6 ninety-eight plants had appeared, of which ninety-four, or 95.9 per cent, were infected.

Halsted (1896:286) has shown how beans planted in ground on which diseased plants were grown the year before, gave from four to six times as many spotted pods as did beans grown on new land; he found also (1896:288 and 1897:330) that mulching the soil with diseased pods from the preceding season caused an increase in the number of spotted pods over those in soil mulched with hay. This would lead to the belief that the fungus is capable of living over winter as spores in the soil or as spores or mycelium in the diseased pods.

Observations were made each year from 1910 to 1914 to determine whether soil which the preceding year had produced plants badly affected with anthracnose could serve as a source of inoculum to seedlings. Healthy seed planted in such soil gave in every instance seedlings that were free from anthracnose and remained so for a considerable time afterward.

Tests were made to determine whether the fungus can live over winter in old pods and vines. Badly spotted pods stored in paper sacks in an attic were found during the late winter and early spring to possess a thin black mycelial growth over their surface outside of the old lesions, and scattered thickly in places on this growth were small black bodies

resembling pycnidia as viewed with a hand lens (fig. 14). A section through these bodies examined under the microscope showed them to be compact

FIG. 14. SAPROPHYTIC DEVELOPMENT OF ANTHRACNOSE ON SURFACE OF DRY PODS

acervuli containing a large number of setae. The conidia, present in large numbers, germinated readily in a nutrient solution, and when healthy plants were inoculated with them anthracnose lesions appeared. The

growth seems to be of a saprophytic nature, as the pods were dry when picked and at that time none of this growth was observed. Other isolations of *C. lindemuthianum* have been made from dry bean pods from time to time, even from pods more than a year old.

Trials were made also to determine whether old pods and vines affected by anthracnose may serve as a source of inoculum to seedlings. In the fall of 1911 a plot of ground where anthracnose had appeared to a severe extent on beans was selected for experiment. The diseased vines were left there, and diseased vines from other places were spread on the plot, all being plowed under the following spring. On June 13 a short row of each of five varieties was planted with seed from selected healthy pods. Adjoining these, one row of each of two varieties was planted with seed spotted with anthracnose. The seedlings were appearing on June 19. In several examinations made before June 25, the plants from the healthy seed showed no affection with anthracnose, while the young leaves of the plants from spotted seed were severely affected. Eight plants from healthy seed were found to be affected on July 1 as shown in table 5. This may have been due to secondary infection. The order in which the varieties appear in the table is the order in which they were planted in the plot.

TABLE 5. RESULTS OF AN EXPERIMENT TO DETERMINE WHETHER OLD PODS AND VINES AFFECTED WITH ANTHRACNOSE CAN SERVE AS A SOURCE OF INOCULUM TO SEEDLINGS

(Seed planted on June 13, 1912; data taken on July 1, 1912)

	Varieties planted with healthy seed					Varieties planted with seed spotted with anthracnose	
	Blue Pod Medium	Turtle Soup	California Cream	Navy Pea	Red Marrow	Navy Pea	Red Marrow
Number of plants appearing.	306	492	346	1,070	1,473	198	262
Number affected with anthracnose.....	0	0	1	2	5	81	95
Per cent affected with anthracnose.....	0	0	0.3	0.2	0.3	41	36

While observations were made each year as to the possibility of infection of seedlings from overwintered vines, no further definite efforts were made to determine this point until the fall of 1915, when a series of experiments

was planned with this end in view. In these experiments the beans were planted in soil in ordinary greenhouse flats. Each flat was numbered, and the conditions involved in the case of each are given herewith. Seeds from healthy pods were used for planting each flat except flat 2, for which seeds spotted with anthracnose were used.

Flat	Description
1	Clean soil
2	Clean soil. Seeds spotted with anthracnose used in planting
3	Contaminated soil
4	Contaminated soil sifted to remove particles of bean tissue
5	Clean soil. Diseased vines and pods from crop of 1915 obtained from disease garden, broken up and mixed with soil in flat
6	Clean soil. Diseased vines and pods from crop of 1915 obtained from disease garden, placed on surface of soil and removed as seedlings were appearing
7	Clean soil. Diseased vines and pods from crop of 1915 obtained from disease garden, placed on surface of soil and left there
8	Clean soil. Diseased vines and pods from crop of 1915 kept in seed house, placed on surface of soil and left there
9	Clean soil. Diseased pods from crop of 1916 kept in seed house, placed on surface of soil and left there

The clean soil (uncontaminated by *C. lindemuthianum*) used was taken from a field where no beans had ever been grown so far as was known, but it was not sterilized except in the last experiment, when it was thought to be contaminated with spores. The flats, unless new, were sterilized with steam. The contaminated soil came from places in the disease garden where bean plants badly affected with anthracnose had grown in 1915. Only the surface soil to a depth of from two to four inches was used. In the first experiment both sifted and unsifted soil was used, but thereafter all contaminated soil was passed through a rather fine sieve in order to remove particles of bean-plant tissue as far as possible.

The healthy seed used was selected from clean pods, and in all but two experiments (II and III) it was immersed for three minutes in a 1–1000 mercuric chloride solution and afterward washed in tap water. This was done to destroy any spores of *C. lindemuthianum* that might possibly be present. The affected seed was disinfected in the same way as was the healthy seed. Seed so badly diseased that it could not germinate was not used. The affected seed used in each experiment was of the same

variety as the healthy seed used. Davis White Wax was used in all experiments except Experiment IV, in which Refugee Wax was used. The old vines and pods affected by anthracnose were of several varieties and no attempt was made to keep them separate. Most of them were well covered with anthracnose lesions. Care was taken to remove all seeds, even shriveled ones, from the pods. The vines and the pods left in the garden over winter were much overrun with numerous saprophytic fungi and were somewhat decomposed by spring. Those kept in the seed house were as intact as they were when placed there.

In setting up an experiment, for example flat 6, the soil was first placed in the flat, the seed was then disinfected and planted usually in four or five rows to a flat, the vines and pods were placed over the surface to a depth of about one and one-half or two inches, the flat was placed in the greenhouse, and tap water was sprinkled on it until the soil was saturated. Unused sphagnum was placed over the flats unmulched by pods or vines in the case of Experiments V and VI. Each flat was prepared separately and every precaution was taken to avoid contaminating one with another.

The temperatures at which the flats were kept in the different experiments varied considerably, but when possible they were kept between 65° and 70° F. This was done in order to favor the fungus and permit infection to take place, and for this reason also the flats were watered more profusely than is best for good germination of bean seed. As a result the germination was very poor in some instances.

Records giving the extent of affection are not included here as they are all very much alike. On nearly every plant the stem was affected with one or more lesions, and often these occurred only at the surface of the ground. A few plants had lesions on the leaves. Lesions on cotyledons coming from the spotted seed used in flat 2 were not considered. The records were usually taken in about three weeks or less after the experiment was set up, in order to get them before secondary infection occurred. There is no doubt that secondary infection did occasionally occur.

These experiments, the results of which are shown in table 6, cannot be regarded as ideal. The results obtained in some cases — for example, from flat 1 in Experiment II — may seem to cast doubt on their reliability. But when the entire series is considered, there can be no doubt that the results show the possibility that old bean pods and vines serve as a source

TABLE 6. RESULTS OF A SERIES OF EXPERIMENTS TO DETERMINE WHETHER CONTAMINATED SOIL OR ANTHRACNOSE-AFFECTED VINES AND PODS OF VARIOUS AGES CAN SERVE AS A SOURCE OF INOCULUM TO BEAN SEEDLINGS

Experiment, and date when set	Flat	Number of plants appearing	Plants affected	
			Number	Per cent
I Nov. 24, 1915	1	12	0	0
	2	47	12	26
	3	24	0	0
	4	35	16	46
	5	24	19	79
	6	17	15	88
	7	14	14	100
II Dec. 29, 1915	1	44	11	25
	2	26	16	62
	4	45	0	0
	5	47	31	66
	6	24	21	88
	7	48	28	58
III April 28, 1916	1	35	0	0
	2	33	16	48
	4	41	0	0
	5	32	2	6
	6	25	5	20
	7	30	4	13
	8	18	15	83
IV June 7, 1916	1	38	0	0
	2	22	21	95
	4	37	0	0
	5	40	2	5
	6	39	1	3
	7	39	35	90
	8	38	34	89
V Nov. 10, 1916	1	34	0	0
	2	26	22	85
	8	31	31	100
	9	38	38	100
VI June 13, 1917	1	8	0	0
	2	17	9	53
	8	12	6	50
	9	72	34	47

of inoculum for the infection of bean seedlings. Apparently soil that is devoid of affected bean tissue cannot serve as a source of inoculum for more than two or three months, or is not an important factor in bringing about infection even though a few spores may live over winter in it.

In order to determine whether old affected vines and pods can serve as a source of inoculum under conditions prevailing out of doors at planting time in the spring, Davis White Wax beans were planted on June 10, 1916, in clean soil in the disease garden; that is to say, in soil in which beans had not been grown since 1911, at which time they were badly affected with anthracnose. Four rows, with forty hills to a row and five seeds to a hill, were planted in the following manner and with the following results (recorded June 26):

Row 1. Seed spotted with anthracnose planted. No mulch used. Only fifteen plants in six hills were alive, all of which showed affection with anthracnose.

Row 2. Clean seed planted, and hills mulched by placing over each a handful of old affected vines left outdoors in a pile over winter. One hundred and sixty-five plants appeared, every one affected on stem or leaves or both.

Row 3. Clean seed planted, and hills mulched by placing over each a handful of old affected vines kept dry in seed house. One hundred and seventy-one plants appeared, every one affected on stem or leaves or both.

Row 4. Clean seed planted. No mulch used. This row was about a rod north of the others. One hundred and sixty-nine plants appeared, on which no infection was observed at this time.

The weather from June 10 to June 15 was clear and warm most of the time and was favorable for seed germination. From the evening of June 15 to June 21 inclusive it was cool and rainy or cloudy, weather very favorable for infection to take place. From June 22 to June 26 inclusive it was clear and warm.

These results plainly indicate that under favorable conditions in the field, affected bean pods and vines from the crop of two preceding years can serve as a source of inoculum when they come into contact with seedlings of a susceptible variety of beans. Nevertheless it is probable that but little infection takes place from contaminated soil or from overwintered vines that are plowed under in preparing the land. In these experiments special pains were taken to place a considerable amount of badly affected

bean tissue where it would be in continued contact with the seedlings. In ordinary practice this would occur only accidentally if at all. But when considerable wet weather follows planting, infection may be expected to occur from contact with old affected vines spread with manure on the surface of the soil after plowing, or from such affected vines as come to the surface after having been plowed under.

Muncie (1917:15–21) carried on tests to determine whether the bean-anthracnose and bean-blight organisms are able to winter over in old bean trash containing affected vines or as spores in the soil. He observed during the summer a small amount of anthracnose on the plants grown in pots where spores had overwintered and where old anthracnose-spotted vines of the second as well as the next preceding year had overwintered. A greater number of plants became affected with blight in these trials. From these data Muncie is convinced that the causal organism of both anthracnose and blight can live over winter in the soil in diseased bean trash and as spores or bacteria in the soil, and infect the crop of the following season. His field observations of preceding years doubtless strengthen this opinion.

Schaffnit (1920) obtained spores with unimpaired germination up to February 12, 1920, from pods of the harvest of the preceding year. Meyer (1910) finds the first appearance of the disease always on plants growing on damp ground directly where fresh stable manure has been applied but not where commercial fertilizers have been used. Pfeiffer (1910), however, believes the organism does not come from manure, as he has observed the disease commonly on land that never receives it. Muncie (1917:21) records inoculations made with an inoculum consisting of dung from a cow fed with bean straw infected by *C. lindemuthianum* and *Bacterium phaseoli*, but states that he was unable in this way to produce anthracnose and that blight appeared on only one plant. It is not unlikely that beans planted on heavily manured ground would produce so rank a growth that moisture conditions about them would be more favorable for infection than with plants not so vigorous. It is also possible for the pathogene to be introduced into a field with manure having infected bean straw mixed with it.

Further infection of the plant and spread of the disease through the field

The inoculation of the leaves, the petioles, the branches, and the inflorescence of the older plants occurs in the same manner as that of

the seedlings. The plants, being larger, are more likely to be in contact with one another and thus make easier the transmission of the spores. If the vines have a tendency to hang low and be bushy, the air beneath them remains sufficiently humid for spore germination for a longer time after rains and dews than does the air outside. During rains the drops of water on the plant run together and move over the surface, in some places dripping from the leaf apices to other leaves and vines, in other places running down the stem or falling in large drops on the pods, where they spread out over the surface as they strike. When wind accompanies a storm, the wet leaves are blown against one another, against the leaves and stems of other plants, or to the ground. If a plant is affected with anthracnose, multitudinous spores from the various lesions become suspended in the rain water and are carried as described to the healthy parts of the plant. The pods become inoculated in this manner and in other ways.

When falling raindrops strike a spore-producing lesion or a film of water anywhere containing spores, drops of the contaminated water are spattered to the near-by stems and leaves. Faulwetter (1917), in his efforts to explain the rapid dissemination of *Bacterium malvacearum*, has made some interesting experiments to determine the distance to which water can be splashed by falling drops of various sizes. He finds that splashing occurs only when drops fall on a film of water, and that it is the water of the film that is splashed. A drop 0.1 cubic centimeter in volume falling 16 feet onto a film over a glass plate spattered water as far as 64 inches. A drop 0.02 cubic centimeter in volume falling 16 feet during a wind of 10 miles an hour "splashed water in abundance a distance of 8 feet.....in moderate quantities as far as 12 feet..... and in slight amounts to 16 feet." He concludes that the possibilities of dissemination of bacteria in suspension in film water on cotton leaves " are considerable if one includes the distance bacteria may be carried from the original lesion, then splashed up again and carried farther, and so on, until a dilution too great for infection is obtained."

In addition to being splashed from contact with falling raindrops, contaminated drops of water may be carried bodily during a heavy wind to healthy parts of the plant, and plants blowing against one another will aid in disseminating the spores. Persons, as well as dogs, rabbits,

pheasants, and other animals, passing through the field when the plants are wet, may serve to carry the spores from one plant to another. Insects, although minor agents, no doubt aid in inoculating healthy plants.

Gardner (1918:34) has shown conclusively that after a rain the spores of *Colletotrichum lagenarium* are present in the soil beneath affected plants, and that they may be disseminated by the spattering of such soil during a rainstorm. He has shown also that spores may be carried across a field in surface water during storms and washed or spattered onto healthy plants, infecting them and thus greatly enlarging the foci of infection.

No field observations of the spread of the bean-anthracnose disease were made during the three years when the writer's field work was done, since the disease appeared to only a slight extent during that time. What has been said regarding the spattering of contaminated water and soil in the dissemination of the two diseases mentioned would seem to be true in the case of *C. lindemuthianum*. Certainly the similarity of this organism and *C. lagenarium* in the matters of spore production, character of spores, and method of infection, would lead to the conclusion that the means of dissemination and inoculation shown in the case of the cucumber-anthracnose organism would exist also in the case of the bean-anthracnose fungus.

Infection of seeds

The appearance and extent of the canker on the seed, and its progress from pod to seed, are described on pages 107 and 111. As the pod matures, the seeds within prepare for a resting period. The cells, now packed with reserve food, become denser, drier, and more capable of resisting decay. The mycelium of the fungus within the cells of the seed also becomes less active, and possibly entirely dormant. It renews its growth, however, at conditions of temperature and humidity to which the embryo of the seed responds but slowly. There is probably very little activity of the fungus in seed stored in a dry place. Halsted (1892:285) and others report having found viable spores on and within spotted seed stored in such a place, and the writer has often so found them. The acervuli were black and dry, and it was not ascertained whether spores were being produced under such conditions or whether they were produced earlier

when the seed was in a more moist condition. Just how long the fungus can live in old seeds has not been determined, although cultures were obtained from seeds two years old.

Infection studies

Susceptibility of plants of different ages to infection

But little evidence has been presented by investigators concerning the susceptibility of plants of different ages to infection. Frank (1883 a: 34) and others find that young and half-grown pods are more susceptible than older ones. Edgerton (1908: 397) remarks that the young bean plant is not readily infected, but his later work (1910: 41) indicates that he had but little trouble in securing infection on seedlings. Cook and Taubenhaus (1912: 49), noting a correlation in this first statement of Edgerton's with results which they had obtained on young fruits of apple and pear with several Gloeosporia attributed by them to the presence of an enzyme capable of forming a tannin-like body toxic to fungi, tested the oxidizing power of the enzyme present in the bean plant at various stages of its development and found that the oxidizing power is greatest in the young bean plant, is small during blossoming and the formation of young pods, is large again when the plants have large green pods, and decreases again when the pods are yellow. After making numerous inoculations on plants at all stages of growth, the writer is convinced that a young bean plant is more susceptible than an older one, and that young parts are more susceptible than older parts. An experiment was made in 1910 in which Refugee Wax beans were planted at intervals of seven and eight days throughout the season, beginning on June 27 and ending on August 22. In the evening of August 31, three days after the beans last planted appeared, all plantings were inoculated by spraying a suspension of spores over all parts of the plants. During the following day the plants were protected as far as possible from drying out by placing wooden boxes over the hills. When observed six days later, all the seedlings were badly infected and some were dying. Good infection was obtained on the younger leaves and petioles of beans planted one month earlier, but slight infection on the older leaves. Those planted two months earlier and having some mature pods were only slightly affected on leaves and vines, but good infection was obtained on young pods. The nearly mature pods showed no evidence of infection. The writer has always obtained

good infection on pods of susceptible varieties when inoculated under favorable conditions for infection before they passed their brittle, or "snap," condition.

Susceptibility of different parts of the plant to infection

As mentioned in the preceding paragraph, Frank (1883 a) says that young bean pods are more subject to attack than are older pods, and this has been noted also by other early writers. Frank further found the pods to be more susceptible than the stems, the leaves, and the petioles, although inoculation on young bush beans resulted in the appearance of lesions on the hypocotyl, the epicotyl, and the veins of young leaves. He found the cotyledons especially susceptible. Scribner (1888) states that parts of the plant other than the pods and the seeds are rarely attacked. Edgerton (1910:42) found that when bean seeds were inoculated with spores of the fig- and the cotton-anthracnose fungi, these organisms were able to attack and grow in the semi-living cotyledons but did not infect other parts of the plants. However, the cotyledons are to be regarded rather as culture media than as host tissue. Lauritzen (1919:33) says the secondary leaves of the bean are more pubescent and seem to be affected more easily at the limiting humidities. This seems to be due to favorable humidity rather than to susceptibility. Others, in writing on the subject, have usually described the disease as occurring on the leaves, the stems, the pods, the seeds, and the cotyledons. The writer has found all young parts of the plant, including the roots, subject to attack, but as they become older they grow more resistant. The tissues of the seedling and of the young pod appear to be the most susceptible. The epicotyl of young bean plants of varieties showing marked resistance to the disease has often become affected when the plant was inoculated, although the other parts showed no lesions. In such cases, resistance may be due to the inability of the infection tube to penetrate the cuticle.

Susceptibility of different varieties of Phaseolus vulgaris L. to infection

In a number of the treatises on bean anthracnose, certain varieties are mentioned as being more susceptible to the disease than other varieties, but in most cases no inoculation experiments have been conducted to confirm these statements. Frank (1883 b:511) says that Lindemuth observed the disease on the red-mottled Zucker-Stangenbohnen while other

varieties near by were not affected, but a few years later he found many varieties susceptible. Trelease (1885), in speaking of the "peculiar susceptibility of the white-podded bean," says that "it is not improbably connected with the delicacy of its tissues, which selection has produced." Scribner (1888) states that wax, or butter, beans — those having yellow pods — are the kind most subject to attack, and later (1889) finds that no variety is exempt, not even those with green pods. McCarthy (1892: 14) says that wax varieties are especially susceptible. Harvey (1894) finds the disease worse on white-podded bush and pole beans. Cobb (1894:379) says that all varieties of *Phaseolus vulgaris* are attacked, though the tenderness of the wax (or butter) beans makes them more susceptible. Halsted (1898:312), after growing six varieties of beans, finds Green Flageolet the most susceptible to anthracnose and blight. Whetzel (1906) states that probably all the "rust-proof" varieties placed on the market will spot under conditions most favorable to the fungus. Tracy (1907), in his notes on varieties, records considerable variation in their susceptibility to anthracnose. Jarvis (1908:162) finds that, while wax-podded varieties are more susceptible, some desirable green-podded beans also are affected. Edgerton (1910:49) finds a number of wax varieties with which he has been working to be very susceptible. He finds Valentine somewhat resistant, and Nox All highly resistant on leaves and stems; and he speaks of Hodson Wax as having a reputation among growers for resistance, although he finds it somewhat susceptible. He thinks that observations of the amount of anthracnose on different varieties growing side by side is of little value in determining their resistance, and believes that the only way to test their resistance in a satisfactory manner is to inoculate each variety with the spores of the fungus. Ferraris (1913) lists a few very susceptible and a few resistant Italian varieties.

The writer (Barrus, 1911) has inoculated a large number of varieties of *Phaseolus vulgaris*. At the time when that work was done, no variety tried proved entirely immune to all cultures. However, it was discovered that there are at least two forms or strains of the organism physiologically different from each other although morphologically and culturally alike. Certain varieties of beans resistant to one of the strains were susceptible to the other, and those resistant to the latter strain were often susceptible to the former. There were other varieties that

were susceptible to all strains, but none were found that were resistant to all. Edgerton and Moreland (1916) inoculated twelve varieties of *P. vulgaris* with cultures of the pathogene from eleven sources and obtained somewhat similar results. The snap varieties generally were susceptible to all cultures, while the Scarlet Runner and a variety which these authors call "Large White Kidney" were resistant to all. Three distinct types of cultures were found among those tried: one able to infect all varieties except the two mentioned; a second that affected the Boston Pea and snap beans but was not able to affect the Red Kidney to any extent; and a third that brought severe infection to the Red Kidney, moderate infection to the snap beans, but only slight infection to the Boston Pea. Fischer (1919:254) records the observations of several German writers concerning the comparative resistance of the different varieties grown in Germany. Some are inclined to think that the wax varieties are more susceptible, others that green snap beans are. Several have observed that pole varieties are more resistant than bush beans, but Fischer says the greater freedom of the former from anthracnose is due to their position on poles, where the conditions are not so favorable for infection as with vines near the ground. He is inclined to believe that the contradictory observations show the existence of different strains of the organism in the various localities. These observations, and those made by him on twenty varieties planted so as to become infected from spotted seed planted among them, lead him to believe that there is no variety in Germany resistant to anthracnose at all times and under all conditions. The most resistant variety of all appears to be Ideal Wachs-Buschbohne. Schaffnit (1920) observed the relative degree of infection on forty-five varieties of beans during 1914 and 1915 at six different localities in Germany, and lists a number of German varieties under each of the following headings: least attacked, moderately attacked, badly attacked. In general he found that varieties descended from the stem "Flageolet" are the most affected, while those descended from Hinrichs Riesen are the least affected; also, that pole beans show much greater resistance than do bush beans. This suggested to him the possibility of crossing pole and bush beans in order to obtain a resistant bush variety. This work he had not completed at the time when he prepared his paper.

The writer (Barrus, 1918) reports the results of a large number of inoculations made on many varieties of *P. vulgaris* and of other beans,

with cultures from fifteen different sources. These for the most part fell into two physiological forms or strains, which are designated, respectively, as *alpha* and *beta*. The varieties of beans, from their behavior when inoculated with these strains, showed a classification into four groups, as follows: ab, those susceptible to either strain of the pathogene; Ab, those resistant to *alpha* but susceptible to *beta*; aB, those susceptible to *alpha* but resistant to *beta*; and AB, those showing resistance to both *alpha* and *beta*. In the first-named group, ab, belong 80 per cent of the wax bush varieties inoculated, 50 per cent of the green-pod bush, 40 per cent of the wax pole beans, and 30 per cent of the green-pod pole beans. It appears from this, then, that the wax bush beans are, generally speaking, the most susceptible to anthracnose. Five varieties are placed in the resistant group AB, but of these only one, Wells' Red Kidney, has shown a satisfactory resistance under all conditions. The writer (Barrus, 1915) described this strain of Red Kidney as having been selected by a farmer as a single healthy individual from a field where all other Red Kidneys were badly affected. This strain has continued to show the same resistance in the many inoculations made by the writer and by other investigators. It is not a pure type, however, the seed varying somewhat in size, shape, and color, and individuals appear from time to time which show some susceptibility to anthracnose, varying from slight to considerable. In a later paper (1918:602) the writer records the resistance of a field bean called White Imperial to several inoculations made with both strains of the pathogene. Recently, however (in 1921), a field of beans said to be White Imperial, the pods of which were severely affected with anthracnose, was observed. It seems not unlikely that strains of the pathogene exist which are capable of infecting even these varieties.

Burkholder (1918:353) has been able to produce an anthracnose-resistant White Marrow by crossing the ordinary susceptible White Marrow with the resistant Wells' Red Kidney and by subsequent selection of the resistant types. In the same manner, McRostie (1919:141) has also reported crossing the Wells' Red Kidney with the Michigan Robust, a white pea bean, but progress had not been made beyond the F_2 generation at the time of this report. In both of these crosses the character of resistance proved to be dominant, and inoculation of the F_3 generation is necessary in order to determine which individuals are homozygous and which are heterozygous to resistance.

No continued efforts have been made, so far as the writer is aware, to render susceptible bean plants immune to anthracnose by the absorption of toxic substances, as has been attempted with some other plants. The writer has endeavored to obtain a greater degree of susceptibility in bean plants showing considerable resistance to one of the strains of *Colletotrichum lindemuthianum*. Such plants, while yet seedlings, were, just previous to inoculation, (a) kept growing in very dry soil for two weeks, (b) kept in very wet soil for two weeks, (c) injured in various ways. In no case was a greater degree of infection obtained than on plants not so treated. Schaffnit (1920) remarks that a weak condition of plants such as comes from a sudden check in growth, as during a sudden fall in temperature, makes them especially susceptible.

Susceptibility of other species of the genus Phaseolus to infection

The statement has sometimes been made that varieties of *Phaseolus vulgaris* only are susceptible to attack by *Colletotrichum lindemuthianum*. Massee (1898), however, reports the disease as most common on French beans (*Phaseolus vulgaris*) and on Scarlet Runner (*P. multiflorus*), and a few other writers on the subject have recorded it as being severe or as occurring on Scarlet Runner (*P. multiflorus*), possibly quoting from Massee (Saccardo 1898, Collinge 1911, Lind 1913). Allescher and Schnabl (1893) distributed specimens of *Gloeosporium lindemuthianum* on leaves of *Phaseolus multiflorus*. Lakon (1916) says that *P. multiflorus* is practically resistant to rust and above all to anthracnose. Schenk (1917) also says that, although the disease is reported as occurring on Feuerbohnen (*P. multiflorus*) in Holland, he has observed this species to be very resistant when other varieties were badly affected. Fischer (1919:258) saw nothing of the disease worth mentioning on three varieties of *P. multiflorus* — *albiflorus* Lam., *coccineus* Lam., and *bicolor* Arrabida — while pole beans of *P. vulgaris* growing next to them were badly affected. Edgerton (1910:41) reports a slight infection of lima beans (*Phaseolus lunatus* var. Small White Pole), and later (with Moreland, 1916:8) good infection on Fordhook's Bush Lima, very slight infection on Large White Kidney, and no infection on Scarlet Runner when inoculated with spores of *Colletotrichum lindemuthianum*. Lind (1913) records the disease on pods, stems, and leaves of *Phaseolus vulgaris*, *P. compressus*, *P. nanus*, and *P. multiflorus*. The

specific name *nanus*, however, refers to the bush forms of *P. vulgaris*, and the name *compressus* to another classification of varieties now included in *P. vulgaris*.

The writer has reported (Barrus, 1918:610) some good infections from inoculations made at various times during several years on the leaves of a number of varieties, both pole and dwarf, of *Phaseolus lunatus* L., both the small, or sieva, lima and the large lima. Fair infections were obtained on the stems, and also, from field inoculations, fair to good infections on the pods (fig. 15). From inoculations made at various times, the varieties Scarlet Runner and White Dutch Runner, of *P. multiflorus* Willd., have shown slight to fair infection on leaves and pods; the latter variety especially showed fair infections on pods (fig. 16) and seeds. The tepary bean, *P. acutifolius* var. *latifolius* G. F. Freeman, has always become badly affected when inoculated in the seedling stage.

The article just cited reports also the results of inoculations made on from one to several varieties of a number of species of Phaseolus supplied by E. V. Piper, of the United States Department of Agriculture. Slight infection was obtained on *Phaseolus aureus* Roxb., but on *P. aconitifolius* Jacq., *P. angularis* (Willd.) W. F. Wight, *P. calcaratus* Roxb., *P. mungo* L., *P. semierectus* L., and *P. sublobatus*, no definite infection resulted.

Susceptibility of plants of other genera and families to infection

Frank (1883 b:518) obtained no infection on cucumbers which he inoculated with anthracnose. Scribner (1888:362) states that the fungus attacks watermelon rinds as well as beans. Farlow and Seymour (1888) and Saccardo (1898:316) record it as occurring on *Citrullus vulgaris* Schrad. Galloway (1889) ascribes the disease "melon rust" to *Gloeosporium lindemuthianum* Sacc. & Magn. Halsted (1893 b:327, 329) obtained infection, from beans, on detached fruits of eggplant, pear, citron, pepper, and persimmon, and he believes (page 333 of reference cited) that the three solanaceous plants, tomato, eggplant, and pepper, are preyed upon by the same *Colletotrichum lindemuthianum* which causes a pod spot of the bean. Stoneman (1898:93) points out that inoculations made on detached fruits placed under a bell jar cannot be depended on, as such fruits are much less resistant to attack than are fruits under normal conditions, and are more in the nature of culture media. Smith (1904:28) obtained good infection from inoculations made on bean, but none on cucumber,

FIG. 15. ANTHRACNOSE ON PODS OF PHASEOLUS LUNATUS, LIMA BEAN

pumpkin, squash, watermelon, and muskmelon. Cook and Taubenhaus (1912:22, 27) obtained only negative results from inoculations of young

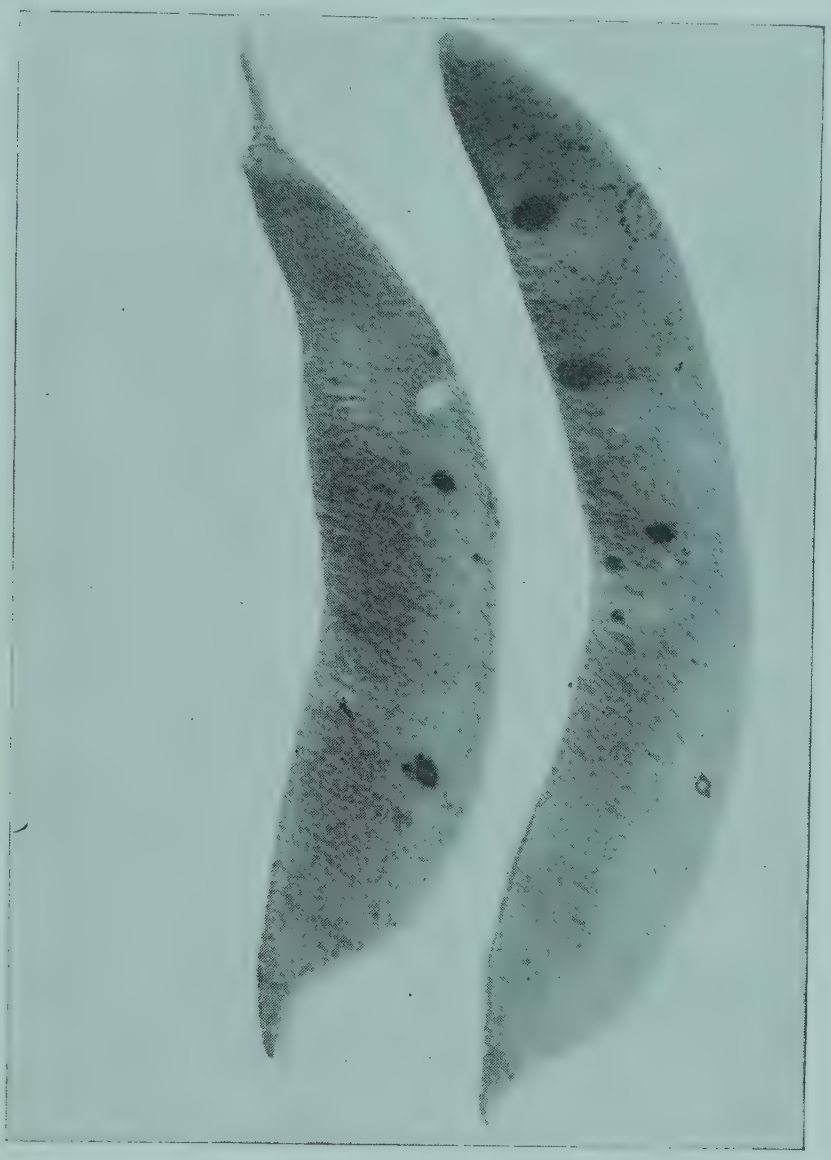

FIG. 16. ANTHRACNOSE ON PODS OF PHASEOLUS MULTIFLORUS VAR. WHITE DUTCH RUNNER, PRODUCED BY ARTIFICIAL INOCULATION MADE ONE MONTH BEFORE PHOTOGRAPH WAS TAKEN

and ripe apples and pears with *C. lindemuthianum*. Edgerton (1911:8) also was unable to infect apples with this organism from inoculations

which he made on picked fruit kept in a moist chamber. He was unsuccessful also in his attempts to infect the leaves, stems, and fruit of cucumbers with this fungus (Edgerton, 1910:41). Shear and Wood (1913:78) inoculated fruit of apple, young wax bean pods, young cotton bolls, a mature pumpkin, a mature squash, green tomato fruits, and a nearly mature watermelon, with the conidia of the bean-anthracnose fungus, punctures being made in all except the bean pod, in which case the spores were applied to the surface; but in no case, not even with the beans, was infection obtained. It is possible that the beans inoculated were resistant to the strain of the pathogene employed. Krüger (1913:294) inoculated beans and cucumber fruits kept under the same bell jar, getting good infection on the beans but none on the cucumber even when it was injured, and he concludes from this that the forms occurring on the two plants are different. Inoculations which he made on apples, bananas, and tomatoes were unsuccessful on the first two, although they resulted in a whitened, sunken, spore-producing area about the punctures.

Chester (1894) reports that many seedlings of cowpea (*Vigna sinensis* Endl.) of the Conch variety died as a result of an attack of anthracnose caused by *Colletotrichum lindemuthianum*, and an examination of the seed showed that 9.5 per cent were diseased. McCarthy (1894:151) reports that pods of cowpeas nearly full-grown were occasionally attacked by a species of Gloeosporium. Butler (1918:262) reports an anthracnose on cowpea in India, saying that in general its characters agree with that of the bean but that experimental work is necessary before the two diseases can be pronounced identical. He records also (page 267 of reference cited) an anthracnose on val (*Dolichos lablab* L.) and on kulthi (*D. biflorus* L.), and tentatively refers the causal pathogene to *Glomerella lindemuthianum* (Sacc. & Magn.) Shear.

Sydow (1886) distributed what appear to be diseased pea pods (labeled *Vicia sativa*) under the name *Gloeosporium lindemuthianum*. Viala and Pacottet (1905) refer to *Colletotrichum lindemuthianum* as the fungus causing anthracnose of peas and beans, and Cooke (1906) reports it as being the cause of a disease of peas as well as of French beans. Other writers have not reported it on peas, and Edgerton (1910:41) could not secure infection from inoculations made on garden peas even after the wax was rubbed off the leaves. Fischer (1919:259) says that both Lemke and Feldt report having observed plants of *Vicia faba* severely attacked

by this fungus, but his own observations do not confirm this and he thinks the disease observed was due to some other fungus.

Edgerton (1910:40) also sprayed spores of *C. lindemuthianum* on young bush beans, alfalfa, and cotton plants protected by bell jars, but obtained infection on the beans alone. Bäumler (1888) reports *Gloeosporium lindemuthianum* as occurring on stems and leaves of *Orobus vernus*. It seems that in this case the species of the pathogene was incorrcetly determined.

The writer, in the course of his infection studies with beans, has inoculated seedlings of sweet pea (*Lathyrus odoratus* L.) and garden pea (*Pisum sativum* L.), vines and young pods of cowpea (*Vigna sinensis* [L.] Endl.), and young plants of mandrake (*Podophyllum peltatum* L.), with spores of *Colletotrichum lindemuthianum*. Excellent infection was obtained on beans used as checks, but the other plants remained free from disease. In a series of other inoculation experiments on seedling plants, fair to good infection resulted on the stems of certain individual black-eyed beans or cowpeas (*Vigna sinensis* [L.] Endl.), and slight to fair infection on the epicotyl of the kulthi bean (*Dolichos biflorus* L.); but no infection resulted on any part of the bonavist bean (*Dolichos lablab* L.), the guar bean (*Cyamopsis tetragonoloba* Taub.), the asparagus bean (*Dolichos sesquipedalis* L.), the jack bean (*Canavalia ensiformis* [D.] DC.), four varieties of horse bean (*Vicia faba* L.), and the garbanzo bean, or chickpea (*Cicer arietinum* L.). There are evidently but few species outside the genus Phaseolus which are susceptible in any degree to anthracnose, and no plants except varieties of *Phaseolus vulgaris* are susceptible to such an extent that the disease becomes epiphytotic in regions where such plants are extensively grown. It is not unlikely that several strains of the pathogene exist, one capable of infecting *Phaseolus multiflorus* or some of its varieties in a severe manner, another able to attack *Vigna sinensis*, and others attacking plants related to the bean, each being confined rather closely to the species, or even to certain varieties within the species, to which they have adapted themselves.

Susceptibility of Phaseolus vulgaris to infection from other anthracnose fungi

Frank (1883 b:518) was the first to inoculate the bean with spores of another anthracnose fungus in order to determine whether the forms occurring on different hosts were really the same species. He sowed

on green bean pods the spores of *Gloeosporium castagna* Mont., which had proved to be very virulent on the leaves of the silver poplar, but obtained no infection. He therefore concluded that gloeosporial forms are independent species and have their own host plants. Southworth (1890:48) attempted unsuccessfully to infect bean pods with the hollyhock-anthracnose fungus, *Colletotrichum althaeae* Southw. (*C. malvarum* [A. Br. & Casp.] Southw.), but was successful with *C. lindemuthianum*. Halsted (1893 b:327, 329), in connection with his cross-inoculation work, obtained good infection on detached bean pods with *Colletotrichum* sp. from the eggplant, and with Gloeosporia from pepper, apple, and tomato; also (1893 d:248) with *Colletotrichum lagernarium* (Pass.) E. & Hals. from the watermelon. Sheldon (1904:132-135) inoculated wax-bean seedlings, bean plants in blossom, and bean pods on the plants, and also six different cucurbits, with spores of *C. lagernarium* from pure cultures obtained from a watermelon fruit. Infection was obtained on the cucurbits in most cases, but the beans for the most part were free from evidence of infection. Sheldon did find, however, spots bearing spores both on the beans inoculated by him and on those used as checks. He decides that it is not safe to conclude from his results that the anthracnose fungus on the beans is the same as that on the melons and the gourds. Edgerton (1910:41) obtained no infection on young bush beans sprayed with spores of the fig anthracnose (*Glomerella fructigena* [Clinton] Sacc.) and of the pepper anthracnose (*G. piperata* [E. & E.] S. & S.), and no infection on freshly picked bean pods placed in a moist chamber and inoculated with a culture of the rose-anthracnose fungus (*Gloeosporium rosae* Hals.); although in every case good infection was obtained with the bean-anthracnose fungus on the beans used as a control. Bean seeds wet with a suspension of spores of the fig- and the cotton-anthracnose fungus were somewhat infected. Spores of the fig-anthracnose fungus were being produced in abundance on seed that had rotted in the ground, and the semi-living cotyledons of the germinating beans were attacked by both fungi. The spots did not develop further, however, while in the case of seeds treated in the same way with spores of the bean-anthracnose fungus the cotyledons, and later the plants, became highly infected. Taubenhaus (1911:198) reports success in obtaining infection on pods of pole and bush lima beans in the field from puncture inoculation with spores of species of Gloeosporium from sweet pea, apple, and mandrake, or may-apple, and with

Gloeosporium officinale E. & E. from sassafras, *G. gallarum* Ch. Rich. from oak gall, and *G. psidii* Del. from guava. The disease produced, except in the last-named case, resembled sweet-pea anthracnose but did not resemble the bean disease. Shear and Wood (1913:77–89) inoculated detached bean pods with anthracnose conidia from avocado, cotton, guava, loquat, mandarin, orange, pitcairnia, and privet, but in the case of none of these did they obtain any infection. Krüger (1913) inoculated detached bean pods kept under bell jars with conidia of gloeosporial forms from apple, banana, and tomato, and, while good infection was obtained on checks consisting of detached fruits of the respective hosts, the result on bean pods was doubtful; no infection was obtained on the uninjured pods, although there was some mycelial growth in the tissue surrounding the injury made on other pods. Gardner (1918:23) inoculated five varieties of beans with *Colletotrichum lagenarium*, with negative results.

On inoculating bean seedlings of several varieties with spores of the anthracnose fungus from sweet pea and from mandrake, the writer did not obtain any infection. Fair infection was obtained on sweet-pea seedlings inoculated with spores of the form from sweet pea, and on the leaves and stems of young mandrake plants growing in the woods and of those transplanted to the greenhouse inoculated with the form from mandrake. From his own results and from those obtained by others, the writer is inclined to believe that, in general, each of the various anthracnose fungi is confined to its own host or to closely related plants.

ECOLOGIC ASPECTS

In the preceding discussion frequent reference has been made to weather conditions favorable to infection. There is no question that the weather is an important factor in the growth of this fungus, just as it is in the growth of higher plants. The fungus has its ups and downs according as the season is wet or dry. Temperature and humidity are the two factors of greatest importance, and of these the latter is usually the controlling one in the Northern States. This has been generally recognized by growers, and its significance in the development of the disease has been pointed out in some of the earlier accounts.

Edgerton (1910:28, and 1915:248) has shown that temperature is the controlling factor under conditions in Louisiana. The disease, while

prevalent during the cooler part of the growing season, is absent from the fields there during the hot months of June, July, and August, even with ample rainfall and when diseased seed was used for planting. Furthermore, Edgerton experienced great difficulty in keeping cultures of the organism alive during the summer. The writer has never had any difficulty in obtaining infections from inoculations made during the summer, although for the success of the experiments he has made them at times when the conditions promised to be most favorable. Some of the inoculations were made in the greenhouse when the temperature during the following days ran high, and yet fair to good infection was obtained in several instances. Cultures of the fungus in the laboratory grow very slowly or not at all during the excessively warm weather of the summer, and in some cases they die when not transferred frequently. When placed in a cellar where the temperature remained at about 16° to 20° C., a good growth of mycelium and abundant production of spores resulted. During the summer season in the North, the periods of excessively high temperatures are short. The high temperature of the day is not sufficient to kill the fungus in the host, and growth and spore production may take place during the lower temperatures of the night. The effect of temperature on growth of the fungus in culture media has already been discussed (page 121). Lauritzen (1919:20), by employing inoculation chambers where temperature and humidity were controlled, determined the range of temperatures at which infection of bean seedlings takes place after inoculation with *Colletotrichum lindemuthianum*, when kept at a favorable constant degree of humidity, to be from 57° to 80° F. At the extremes the number of infections occurring are small, but they are more abundant at the more nearly optimum temperatures, as one would expect. Lauritzen says that the data point to a lower temperature limit for infection when forty-eight hours are used for the infection period than when twenty-four hours are used.

Moisture must be present or the humidity of the air high if the fungus is to gain entrance to the host. Lauritzen (1919:29) found that infection took place at humidities of 95.8 and above when the temperature was kept at from 65° to 68° F. It was not necessary that a film of moisture be kept on the leaf during the germination of the spore, for infection occurred when the plants were dried off after inoculation and before being placed in the inoculation chamber. Lauritzen did not determine how

the spore gets sufficient water in such cases to permit germination, but he suggests that when the evaporation is not too great it may absorb water from the host plant by imbibition and later by osmosis.

If the soil is wet and cold, the bean seed germinates slowly, but the spores of the fungus when present on the seed under such conditions will germinate and penetrate the host before it appears above ground. If dry weather follows the appearance of the plants grown from spotted seed and infection has not yet taken place, the chances are good that the spotted cotyledons will drop off before any infection occurs. When this happens the plants are as free from infection as though they had come from healthy seed, but the affected cotyledons on the ground may serve as a source of inoculum for a time. Often after wet weather the juvenile leaves of the seedlings become very badly spotted. These in turn drop off, and if the plant has not been infected otherwise it may continue to develop entirely free of the disease (fig. 17). If, on the other hand, rainy weather should occur following the germination of spotted seed and before the cotyledons fall, some of the seedlings will surely become infected and the disease will be likely to spread to neighboring plants. In fact, an instance is known in which, of two fields planted from the same lot of seed but at different times, one field became badly diseased and the other remained healthy because rainy weather succeeded the planting of the one and dry weather the planting of the other.

If infection is to take place in plants inoculated with the spores of the fungus, a moist condition must prevail for at least eighteen consecutive hours at some time before the spores succumb to desiccation so that they may germinate and form appressoria. This statement is based on spore-germination tests recorded earlier (page 117). In the inoculation experiments conducted by the writer, the plants were usually kept in an inoculation chamber for about forty-eight hours, although successful results were obtained when they were left for but twenty-four hours. That the spores may endure a period of dryness before favorable conditions arrive was shown by an experiment in which seedlings growing outdoors were inoculated during the morning of a bright, hot day. The next morning, before the dew had evaporated, each plant was covered with a shaded lamp chimney plugged with cotton at the upper end. All these plants showed lesions after six days.

FIG. 17. BEAN PLANT FROM SPOTTED SEED, THE JUVENILE LEAVES AND STEM OF WHICH BECAME AFFECTED WITH ANTHRACNOSE BUT WHICH PRODUCED A CLEAN CROP OF PODS BECAUSE DRY WEATHER PREVAILED DURING THE SUMMER

(Transplanted to a pot for photographing)

A rainy period of several days accompanied by cool weather is the most favorable condition for infection and for the development of the fungus. Night dew or even humid air, however, is sufficient to allow infection to take place. Conditions permitting the plant to retain moisture beneath the vines are particularly favorable for the infection of the pods. Such conditions are afforded by poor soil drainage, or especially by poor air drainage such as may come about from a bushy growth of vines and from plants growing close together; and similar conditions may exist in a low area or pocket in the field.

Beans grown at the time of the year when the prevailing weather conditions are the least likely to be favorable for infection, will of course be the freest from anthracnose. Plants inoculated artificially during a rainy day will become badly diseased, while plants in neighboring hills in the same row will be but slightly affected and hills farther on not at all. This is because the weather has remained comparatively dry from the time of inoculation until the pods were maturing, and thus spore dissemination was prevented. The disease does not spread as readily through a field planted in check rows as through one planted in drills. Corbett (1907) says that growers of field beans find the disease worse on crops planted early. In New York State late-maturing beans are the most liable to damage from anthracnose, as weather conditions favorable for infection commonly occur during September. For this reason an early-maturing variety planted early would have a better chance of escaping infection, other things being equal, than a late-maturing one.

These facts explain why the disease materially decreased during the dry seasons of the four years from 1907 to 1910, and why it has been so severe during years of abundant rainfall. The seed produced in dry seasons is practically free from the disease, and when such seed is used the plants resulting therefrom are remarkably free from anthracnose, even though the season may be wet, because the source of infection is not present. After a season or so of rainy weather, however, the disease, at first inconspicuous, may become general throughout the field and a large amount of spotted seed may result. It has been claimed by seedsmen that in certain irrigated sections of the West where there is but little rainfall during the growing season, plants free from the disease can be grown from spotted seed; but it is questionable whether the moist conditions beneath the vines resulting from irrigation would not be sufficiently

favorable for infection occasionally to take place, at least when spotted seed is planted. The disease is occasionally reported from such sections. Complete freedom from anthracnose may be expected in those regions where dry farming is practiced. Lauritzen (1919:32) suggests that the variation in the amount of moisture in the air in different regions may be an important factor in the distribution of diseases over the earth's surface.

PROPHYLACTIC ASPECTS

As early as 1893 a number of measures for the control of bean anthracnose had been recommended. Among these were such as treating seed with chemicals or hot water, selecting seed from healthy plants, spraying with bordeaux mixture and other substances, working among the plants only when they are dry, planting exclusively on ground that has not produced diseased plants the year before, and selecting a dry, airy situation with light soil. These recommendations, if carefully followed, will usually result in the production of plants free from anthracnose. Doubt has been cast, however, on the efficacy of certain of these recommendations, and it is worth while to consider the advantages and disadvantages of the various methods.

Seed disinfection

Seed treatment was first recommended by Halsted (1892:286), who at that time used ammoniacal copper carbonate. Later (Halsted and Kelsey, 1895:30) he tried full-, half-, and quarter-strength bordeaux mixture, and concluded that such treatment had but little effect in killing the mycelium within the seed. Beach (1892:320), after experimenting with hot water, bordeaux, ammoniacal copper carbonate, and potassium sulfide, found that, while hot-water treatment resulted in the lowest percentage of plants with anthracnose, the untreated seed gave a greater quantity of marketable beans because of the better stand, and that even with severe treatment, enough disease remained to injure the crop. Craig (1893), after soaking seed for varying lengths of time in solutions of different strengths of ammoniacal copper carbonate and copper sulfate, concluded that seed can be treated cheaply and advantageously with copper compounds, preferably ammoniacal copper carbonate. The best result he obtained, however, was but 79 per cent of healthy plants, and but 73 per cent of the treated seed germinated. Later (1898) he experimented with lysol,

formalin, potassium sulfide, nitrate of soda, corrosive sublimate, and kainit. The lysol treatment resulted in 4 per cent of diseased pods, in comparison with 57 per cent in the check row. The value of other treatments are in the order named, corrosive sublimate giving 19 per cent of diseased pods and kainit 36 per cent. Bedford (1900) soaked bean seed for two hours in formalin solutions varying from one ounce in one gallon of water to one ounce in four gallons. The former dilution gave the better results, without the germination being affected appreciably. Sevey (1907) states that experiments at Cornell University, in which bean seed was soaked for forty-five minutes in formalin solution 1–200, gave profitable results. Kirk (1905) says that good results have been obtained by soaking seed for five minutes in water at a temperature of 140° F. (60° C.), or for fifteen minutes in water at 130° F. (54.4° C.).

Whetzel (1906) believes seed treatment to be of little practical value in controlling the disease, as such treatment reduces the stand and renders the seeds unfit for planting with a machine unless they are allowed to dry, in which case many of them slip their coats and thus become worthless. Fulton (1908:15) says that he has kept beans for forty-five minutes at 135° F. (57.2° C.) dry heat without appreciable effect on germination, while seeds placed in water during a like exposure are practically all killed. He thought that dry heat might be used as a seed treatment for control of bacterial blight, but experiments that he made to prove this gave negative results. Edgerton (1910:46–48), from experiments he has made, is inclined to believe that the disease may be materially reduced by soaking the seed for from ten to fifteen minutes in water at a temperature of 50° C. (122° F.), and that seeds thus treated will not slip their coats and their germinative ability is not impaired. Later, Edgerton and Moreland (1913) report that the treatment of bean seed with hot water 50° C. for eight minutes, with corrosive sublimate solution 1–1000 for twenty minutes, with benetol solution 1–50 for twenty minutes, or with corrosive sublimate 1–1000 in a 1–50 glycerin solution, did not materially reduce the percentage of germination below that of untreated seed, although formaldehyde solution 1–100 did reduce the germination in the field. However, none of the treatments except hot water had much merit as a control measure for anthracnose, although blight was materially reduced by the treatments with corrosive sublimate and benetol.

Hollman (1915:691) treated seed with 2.5- and 1.25-per-cent Chlorphenolquecksilber, with 1- and 2-per-cent sublimate, with 2.5- and 4-per-cent formalin, with a tar preparation called "Körnerschutz," with petroleum for thirty minutes, and with 2-per-cent copper sulfate, and also with 1-per-cent bordeaux sprayed on the seeds. None of these treatments were effective, the disease being serious in all plots. The Chlorphenolquecksilber seemed to have the effect of stimulating the plants to increased growth, so that they yielded more, in spite of the disease, than did plants in other plots.

Fischer (1919:249) discusses the results obtained by a number of investigators with seed treatment. He says that Appel used 1-per-cent sublimate; Remn and Vasters tried Chlorphenolquecksilber; Wahl tried a new and water-free Chlorphenolquecksilber called "Uspulun"; Weirup experimented with sublimate and later with Uspulun; Schander and Krause treated badly affected seed, which when untreated gave but 19.3 per cent germination, with 1-per-cent sublimate for fifteen minutes, resulting in 29.3 per cent germination; with 0.25-per-cent Chinosol for three hours, resulting in 32 per cent germination; and with 5-per-cent Uspulun for one and one-half hours, resulting in 46 per cent germination. In no case, however, was there a satisfactory control of the disease, which became general throughout all the plots. Even when an entire field at the experiment station was planted with treated seed — in which case infection could not have taken place from near-by plants from untreated seed — the disease appeared just as severely as in fields planted with untreated seed. Fischer concludes from these observations that seed treatment of beans to control anthracnose has no practical value.

Muncie (1917:26–37) treated seed for varying lengths of time with chemicals of varying strengths, and with both dry heat and hot water. The chemicals used were: mercuric chloride and sodium nitrate heated to 55° C. (131° F.) and not heated; mercuric chloride alone; mercuric chloride with oxalic acid; zinc chloride; formaldehyde solution as a dip and sprinkled on seed; formaldehyde gas; copper sulfate with the addition of sulfuric acid; and calcium hypochlorite. Both healthy seed, and seed affected with anthracnose and with blight, were treated, and the effect of the treatment on germination and on the pathogenes was noted. It is seen from the results given that in none of the treatments was either pathogene killed in all the seeds, except in those cases in which the

treatment materially reduced the percentage of germination. Muncie states, in summing up the results of the treatments, that it seems possible to control the disease in a large degree in case of a light infection by employing seed treatments, and that the treatment most efficient is either a thirty-minutes immersion in a 35-per-cent solution of bleaching powder, or a sprinkling of the seed, as in the treatment of oat smut, with a solution of formaldehyde, using 1 pint of formaldehyde to 30 gallons of water. There is not sufficient evidence submitted in his data, however, to admit this possibility. His summary at the end of the bulletin states accurately the conclusions reached, namely, "Seed treatments with chemical solutions and wet and dry heat have failed to control these diseases." Rapp (1920) concludes from his numerous seed-treatment experiments with formaldehyde, mercuric chloride, sulfuric acid, dry heat, and hot water, to control bacterial blight, that no present method can be regarded as satisfactory, since in killing the blight pathogene the germinating power of the seed is either greatly weakened or totally destroyed.

Kidd and West (1918) soaked bean and other seeds for varying lengths of time (from six to seventy-two hours), and found that, while germination was more rapid from soaked than from unsoaked seeds, subsequent growth, particularly of the bean, was poorer — although with horse beans (*Vicia faba*) it was greatly improved. Bean seed was soaked in water at various temperatures, but always the resultant growth was poorer than when dry seed was used. The literature on the subject, however, reviewed by Kidd and West (1919), indicates a better growth and a higher total yield from soaking in a limited quantity of water.

Further experimentation with seed treatment should not be regarded as something bound to be resultless. No one has made a careful study of the permeability of the seed coat of the bean to various disinfecting agencies, nor of the action of these agencies on the fungus within the seed. Seed treatment, to be effective, must destroy the pathogene within the seed, notwithstanding the extent of its growth there, in order that the affected seed may not serve as a source of inoculum. At the same time, the treatment must not injure sound seed. Any treatment, to be of value, must achieve these two conditions, and the problem does not appear to be insurmountable. Nevertheless, healthy seed can be obtained in other ways. The selection of clean seed (page 168) certainly offers a greater promise of success.

Sorting out affected seed

The selection of clean seed has been recommended by many plant pathologists. Frank (1883b:523), after having determined that infection of the seedling can take place from the fungus overwintered in affected seed, was the first person to recommend the use of clean seed by the sorting-out of spotted ones or by the securing of seed from non-infested fields. Beach (1892:323-326) obtained good results by sorting out the affected seed before planting. Gain (1898:200), after experimenting with Mont d'Or, a climbing wax-podded variety with dark brown seeds, states that he is able to discard practically every diseased seed by hand-sorting. He observes that diseased seeds are lighter than healthy ones, and advises growers to discard all light seed. In another article (1899:389) he says that by carefully sorting out infected seed the anthracnose disease can be controlled. Whetzel (1908:432), however, although he used the utmost care to remove every suspected bean, was unable to remove the diseased seed completely from white beans, a germination test of the seed thus sorted showing as many as 12 per cent of the remaining seed diseased. When an attempt is made to sort colored seed, an even larger percentage of diseased seed passes unobserved. Fischer (1919:252) concludes from experiments conducted by Schander and Krause, and from other tests made at Bromberg in 1915 and 1916, that it is not possible to control the disease by this method since many affected seeds cannot be detected from their appearance.

It is, of course, impossible to sort out every affected seed even by the most careful examination. Such seed as are left in may produce affected plants if conditions following planting are favorable for the development of the fungus, and such affected plants may serve as a source of inoculum to other plants in the field. However, as every diseased seed discarded removes one source from the field, it would appear to be preferable to sort the seed carefully before planting rather than not to sort at all. A practical grower of a considerable acreage of beans in northern Vermont says that since he has made a practice of hand-sorting his seed he has had no anthracnose, but that before he did so the disease was harmful.

Selecting seed from clean pods

It has occurred to a number of experimenters that the surest way of obtaining clean seed is to select it from healthy plants or at least from

unspotted pods. Harvey (1894) advises this method, and emphasizes the idea that pods showing any evidence of disease, such as pits, discolored patches, and wrinkled or blistered places, should be rejected. Cobb (1894: 383) recommends hand-picking the seed in the field, selecting only the healthiest-looking pods. Several others since then have recommended the practice. For several years Whetzel (1908:441) grew clean Black Wax beans that were selected from clean pods, and at a time when anthracnose was very prevalent throughout the State. He recommends selecting seed from clean pods, hand-picking them in the field, and resorting them later. He suggests also that seed from the irrigated regions of the West may possibly be free from the disease. A seedsman in an irrigated section of Colorado declares that he has been able to grow clean plants from diseased seed and could continue the practice without danger of the disease appearing in the field.

The writer selected seed from clean pods during four consecutive seasons (1908 to 1911), the purpose being to determine whether such seed would produce anthracnose-free plants with ordinary culture, particularly during a wet season, and whether such a method could be recommended as a general farm practice, Since 1911 he has been unable to carry out these trials further, except in a most limited way.

The seed for these experiments was obtained from pods picked in the field, or in a few cases from the mow. Any seeds showing evidence of anthracnose or blight were rejected. Later the pods were resorted, and, after shelling, the beans also were sorted to remove broken, undersized, or abnormal beans. The seed was then distributed, in lots of about a quart of each variety, to growers and experimenters in this and other States, in order to obtain, in some place at least, good conditions for a test. Those who received the seed were urged to plant it at a distance from other bean patches and to observe the precautions necessary to avoid communication of the disease to this seed patch.

In these tests extending over a period of four years, twenty-four different plots of beans, containing from one to eight varieties, were grown in various parts of New York State and in a few places outside the State. In five of these plots, there was some anthracnose on a few of the varieties. In all but one of these five cases the infection was slight, and in all cases the inoculum came from a source other than the seed.

The chief drawback to the success of the trials was the dry weather which prevailed during the growing season in these years. Beans grown from seed that had not been selected produced anthracnose-free plants in many cases. Plants grown by Dr. Edgerton in Louisiana from healthy seed sent to him were free from anthracnose and with few exceptions free from blight, while other beans grown in the trucking section were badly affected with both anthracnose and blight.

Another factor not given consideration at that time was the resistance of many of these varieties to at least one strain of the pathogene. It was learned later that this is true of the varieties Navy Pea, White Kidney, Red Kidney, Red Marrow, and Blue Pod Medium, and also of Turtle Soup to some extent. In most instances, however, anthracnose had in the past appeared in a destructive manner on the varieties sent for testing, in the localities under consideration.

The introduction of healthy seed of a certain variety into a locality in which the strain of the fungus to which it is susceptible is absent, would of necessity result in an anthracnose-free crop. This may be the reason why clean seed from other sections of the country often produces better yields than does home-grown seed. However, if affected seed of such a variety is introduced into a certain locality, the strain of the pathogene present on the seed, being capable of producing the disease in that variety, will multiply under conditions favorable for it and the entire crop may become diseased. Healthy seed is therefore always safer to use as long as the particular variety is susceptible to any strain of the organism.

In 1914 Professor F. C. Stewart, of Geneva, New York, planted seed that he himself had selected from clean pods. The plants remained healthy all summer and the pods were free from anthracnose when picked. A patch of Red Kidney and Turtle Soup beans selected from seed from clean pods in 1912 was planted at Ithaca at a distance of ten rods from other beans artificially inoculated with the two strains of *Colletotrichum lindemuthianum* during the summer. The plants from clean seed remained free from anthracnose.

In 1915 Bert Smalley, of Interlaken, New York, grew one row, fifteen rods long, of Red Marrow beans from seed selected from clean pods by Professor Stewart and afterward resorted by him in order to be sure there was no anthracnose present. The field in which this row of Red Marrows was grown was not cultivated at all during the season because of wet

weather, and so weeds of various kinds grew up among the bean plants. On October 4 the plants were found to be generally affected with anthracnose. From the row 75 plants were selected, one plant at every pace. On these plants there were 209 pods, of which 137 were affected with anthracnose, 67 were not spotted, and 5 were doubtful. About 40 rods southwest of the end of this row was a large field of Red Kidney beans which were badly affected with anthracnose. It was concluded that the first infection of plants in the row planted with clean seed came from spores carried from the affected Red Kidneys by some animal, and, since the tall weeds about the beans kept them moist most of the time during the rainy season, and since they were planted in drills so that the plants were in contact with one another, the disease readily spread along the entire row.

These trials seem to indicate that the use of clean seed is not altogether successful in producing a crop of beans free from anthracnose unless the season is dry, under which condition there is no loss from the disease in any field. The experiments are reported because the results are such as may be expected in such cases. So far as observations were made in these and in other experiments, clean seed always produced anthracnose-free seedlings in the field, and this is all that can be expected of clean seed. Infection, when present, must have taken place from an inoculum of a source other than the seed. In some cases this came early from old affected vines or from near-by affected plants. Infection will always be likely to occur from such sources under favorable weather conditions unless precautions are taken to prevent it. Since clean seed can be depended upon to produce seedlings free from anthracnose, the question becomes one of deciding whether or not the presence of affected seedlings in the field is a sufficiently great menace to warrant the use of clean seed. The writer, from observations of his own experimental plots and of many fields in which clean seed as compared with affected seed has been used, is convinced that the presence of such affected seedlings is a menace that warrants the grower's going to considerable pains and expense in order to obtain healthy seed. Growers generally will probably prefer to buy clean seed if they can get it, rather than to take the trouble to produce it. But some one must produce it if it is to be had, and the question of production is the one concerned here. It is true that following dry seasons there will be but little difficulty in obtaining

bean seed almost or quite free from anthracnose. But it must be possible to obtain such seed every year if the disease is to be avoided in years favorable for its appearance. The practice of selecting from clean pods is the only reliable way to secure seed free from anthracnose (figs. 18 and 19). The method in its practical application involves the use of a seed plot, on which the selected clean seed is planted. This plot should

FIG. 18. A HILL OF WAX BEANS FROM SPOTTED SEED
The pods are so badly affected with anthracnose that they are worthless

produce the necessary seed for planting the main field the following year. The steps in carrying out the measure are as follows:

1. Selection, in the fall, of pods having no anthracnose or blight spots. These should be shelled by hand or with a flail, and the seed afterward sorted over to remove all discolored, impure, undersized, shriveled, or broken beans. The amount of seed to be selected in this way will depend on the amount needed for planting the main field. If 40 bushels of seed are required for planting the main field and 20 bushels an acre can be

expected from the seed plot, then enough seed must be selected from clean pods to plant two acres.

When the main field contains 200 acres or more, the size of a plot necessary to produce sufficient seed for the main field will be so large that

FIG. 19. A HILL OF WAX BEANS FROM HEALTHY SEED
The pods are entirely free from anthracnose

it will be difficult to obtain by pod selection enough seed to plant it. In such a case it is desirable to maintain an increase plot in addition to a small seed plot. The seed plot would be used to provide clean seed for the increase plot, which in turn would produce sufficient seed for the

main field. This plan would require two years to get seed for the main field, but would afterward permit an economy of time and effort.

2. Location of the seed plot at a considerable distance, preferably 40 rods or more, from other bean fields or garden patches containing beans. If an increase plot is used, it should be located at some distance from the seed plot and also at some distance from the main field. This is to prevent, as far as possible, the transfer of spores of the causal fungus from infected plants to plants in the seed plot. The shorter the distance between the seed plot and beans growing elsewhere, other things being equal, the greater is the chance that the beans in the seed plot will become inoculated.

3. Location of the seed plot and the bean field on soil on which beans were not produced the preceding year.

4. Cultivation of the seed plot before the cultivation of other beans when the same tool is used for both; or, better, reservation for the seed plot of a cultivator not used in other bean fields.

5. The precaution of not visiting the seed plot when vines or soil are wet. This precaution should apply to all bean fields. Care should be taken, even when the vines are dry, not to go directly into the seed plot from other bean fields.

6. Prompt removal and destruction of any plants in the seed plot found to be affected with anthracnose.

7. Application of bordeaux mixture to the plants in the seed plot several times during the season, in order to prevent infection from spores that may be carried there.

8. Selection, before the beans are harvested, of clean and otherwise desirable pods from the seed plot or other fields, in order to obtain healthy seed for planting the succeeding year's seed plot.

9. Careful harvesting of the bean plants in the seed plot and their storage in a place separate from other bean vines.

10. The threshing of the beans with a flail or in other ways so that a mixture with other bean seed cannot take place.

11. Storage of the seed in a cool, dry place until planting time the succeeding year.

12. Careful hand-picking of this seed for the increase plot or the main field in order to remove all discolored or otherwise unsatisfactory seed.

This method of controlling anthracnose in the main field will cost less than spraying five times, and is more certain of success. Much of the procedure costs nothing, but merely requires not doing certain things. The labor involved in growing a 40-acre field of beans by this method, above that ordinarily required for growing such a field, consists in selecting sufficient seed for a seed plot, in spraying the vines in this plot, in removing affected plants from it when present, in the separate harvesting and threshing of the crop, and in the careful hand-picking of the seed from it. Other work done in connection with the seed plot would have been required had it been a part of the main field.

If home-grown seed is as good as or superior to that purchased elsewhere, then growers of a large acreage of beans who have felt the loss from anthracnose, or seed dealers who are desirous of obtaining the best possible seed for their territory, should give consideration to this method. It is not to be expected that many farmers will adopt such a method, because of the detail required in order to insure success. It should be pointed out here that this method cannot be depended upon absolutely to control bacterial blight. Burkholder (1921:67) states that as a result of systemic infection of the bean plant the seeds may become infected without the pods around them showing any evidence of blight.

Procuring seed from localities where anthracnose does not occur

Observations were made for two seasons (1908 and 1909) of fields planted with Colorado-grown and eastern-grown Refugee Wax bean seed. There was no anthracnose but considerable blight present in the field planted with the western seed, while anthracnose was present to some extent in the field planted with the eastern seed. The seed procured from Colorado the second year was dry and split easily, and besides it germinated poorly, and so the yield was lower than that from the eastern seed. Edgerton (1910:50) has planted Colorado seed in Louisiana and has found it freer from anthracnose than most other seed, though much more severely affected with bacterial blight. Muncie (1917:41) reports trials in Michigan of seed grown for one year in the States of Washington, Idaho, and California. There was a little anthracnose in the seed returned from Washington but none in that from the other States. Idaho-grown seed gave very satisfactory results the first year but poor results the second year, largely because the seed was immature due to an early frost.

California-grown Early Wonder seed gave excellent results, and the plants ripened two weeks earlier in Michigan than did plants of the same variety from seed grown in Idaho and from seed grown in Michigan. Muncie believes that carefully selected seed sent to southern California to be grown for one year for seed purposes, will furnish a supply of seed year after year that will be superior to Michigan-grown seed.

Edgerton (1910:28–37) states that at the high summer temperatures in Louisiana, bean anthracnose does not develop even when spotted seed is planted; and later he suggests (Edgerton and Moreland, 1913:17) that Louisiana truckers grow their own bean seed during the summer as a second crop and thus secure seed freer from disease than that purchased from the North.

The question whether eastern growers would have better success in buying western seed than by the use of eastern-grown seed is still unanswered. It must be considered from other standpoints as well as from that of controlling anthracnose. It is true that this disease does not occur as commonly or cause as much damage in the West as in the East. It was, however, rather prevalent in Colorado in 1916 and 1917, and to an extent sufficient to cause some spotting of the seed. Bacterial blight occurs rather commonly in the West, so that one cannot depend on western seed being free from this disease. Nevertheless, eastern seedsmen have found that they can depend upon getting good seed from the West oftener than from the East, and the bean-seed-growing industry has developed rapidly in Colorado and Idaho in recent years. Most of the seed beans grown are garden and canning varieties, which command a much higher price in the East than the ordinary field sorts.

Avoiding conditions favorable for the dissemination and growth of the fungus

If it becomes necessary to plant seed having a small percentage of anthracnose infection, or if the disease appears in the field from an outside source of inoculum, or even when clean seed is planted, it is advisable to avoid as far as is practicable those conditions which favor the spread of the pathogene. Healthy plants have been grown from clean seed in experimental plots in the same field with plants that have become badly diseased from artificial inoculation with the anthracnose fungus. It has been observed also in a large number of instances that plants in hills next to inoculated plants often did not become infected although

the weather was favorable for infection to take place. The disease did not spread because certain conditions favorable for it were not allowed to exist. Some of the precautions to be taken are considered in the following pages.

Manner of planting

Beans planted so close together that they form a dense mat of vines favor the spread of the disease. The vines obstruct cultivation and do not allow either the wind or the sunshine to dry out the moisture beneath them. Spores of the pathogene, if present, are transferred from one plant to others in contact, and are able under the moist conditions to germinate and penetrate the tissues of the host without difficulty.

The different varieties vary so much in their habit of growth and in the size of their seed that it is impossible to give a general recommendation for planting. Halsted (Halsted and Kelsey, 1895:28, and Halsted, 1897: 290) planted seed from 3 to 24 inches apart in rows 20 inches apart. There was a considerable decline in the proportion of spotted pods and also in the total yield of pods as the distance between the plants was increased. Halsey concludes that $4\frac{1}{2}$ inches is the most satisfactory distance for Golden Wax beans. Ferris (1909:8) recommends, in addition to selecting clean seed, planting the beans in bunches in the row far enough apart so that the clusters do not touch one another. Edgerton (1909:5) finds three beans to the hill, and the hills 18 inches apart, a very satisfactory planting distance for beans grown in Louisiana. Fischer (1919) says that Riehm suggests planting in hills 50 by 50 centimeters apart instead of in drills, in order to permit good air drainage. Von Diakonoff (1909) suggests planting the rows parallel to the direction of the prevailing winds in order that the plants may be well aërated.

Anthracnose will not spread through a field of beans planted in hills as rapidly as it will through one planted in drills, because the vines in one hill are somewhat isolated from vines in other hills for a considerable part of the season, whereas in drills there is a continuous row of plants in contact with one another, and anthracnose starting at any point in the row would, under favorable conditions, spread the entire length. To secure maximum protection by hill planting, the hills should be far enough apart each way so that the vines of one hill will not come in contact with vines of other hills; and this distance will vary with different

varieties. Of course the yield in such a case will be reduced below that obtained when a greater amount of seed is used, but not proportionately. It is impracticable, however, to plant hills at a distance sufficient to keep the vines of one hill from touching those of others during the latter part of the season. Just what distance apart the hills of any variety should be planted in order to secure a satisfactory yield and protection from infection has not been determined. Whatever has been said on this subject should be considered also in the light of present knowledge concerning the possibility of spore dissemination by spattering.

Good land drainage

The relation of drainage to bean anthracnose is obvious. Poorly drained soil is cold, and bean seed planted in such soil starts slowly or not at all. If the seed is diseased, the fungus develops rapidly and usually destroys the seedling before it appears above ground. During a wet season poorly drained soil tends to produce a moist condition about the base of the plants, which should be avoided. Galloway (1889) notes that the disease is worse on moist soil. Cobb (1894:383) and Querner (1908), in recommending control measures for the disease, suggest draining the land, and others suggest not choosing low, damp ground.

Removal of affected seedlings

Affected seedlings serve as a source of infection to healthy plants in the field and the garden. An early removal of them would aid in lessening the amount of disease should favorable weather for infection follow. The practice of removing affected plants was early recommended. Berkeley (1880) suggests that diseased plants be pulled and burned, and many other writers on the subject have recommended this. Whetzel (1908:433), however, has pointed out that this method is absolutely impracticable except in short garden rows. It is, of course, out of the question to attempt to remove affected seedlings from a field. However, in the seed plot and in the garden it is worth while to remove and destroy such plants, as is explained later. If the weather remains dry following the appearance of the seedling, the diseased cotyledons will drop off before further infection of the seedling takes place, as already noted (page 161). In such a case the field would be as free from disease as though every diseased seedling had been removed. Appel (1916) has

observed that hilling young plants tends to prevent the spread of the disease by covering the lesions at the base of the stem, thus hindering the spores from escaping. The small lesions heal afterward, and, while the larger ones may develop and rot the plant, the spores produced are not able to be disseminated. Edgerton (1909:5) suggests that danger of the disease's spreading from affected seedlings may be lessened if the field is not entered until the cotyledons have dropped off.

Leaving the plants untouched while wet

As has been noted (page 176), a diseased plant may exist in a field of beans without the disease spreading materially to other plants. If, however, when the plants are wet, some agent passing through the field comes in contact with the diseased vine, spores are likely to be distributed to plants beyond. A very active agent in distributing spores is a horse and cultivator, or, even more so, a person picking beans. Growers of a large acreage like to start work in the fields early, and yet there are many mornings during the growing season when the dew remains on the plants until after nine o'clock. It is very important that operations in the bean field should be postponed until the vines are dry. The observance of this simple precaution will do much toward preventing a general infection of the field.

Destroying diseased vines in the fall

Since the fungus lives over winter on the old pods and vines, these may serve as a source of infection to young beans growing near them the following spring. Galloway (1889) recommends the burning of all diseased vines and pods. Both Harvey (1894) and Cobb (1894:383) believe it advisable to remove and destroy all diseased vines after harvest if the same land is to be used for beans the following year. Whetzel (1906:209) states that diseased pods and stalks should be removed from the field. The old vines and pods are not so often a source of inoculum as are the affected seeds, and yet it is unwise to disregard them altogether. One should not go to a considerable expense to remove and destroy old affected vines from the field, but should prevent their coming into contact with the new crop as far as it is practicable to do so. A rotation of the bean crop, and the application of manure containing bean refuse to other than the current or the following year's bean field, are helpful measures.

Planting at a time of the year when anthracnose is least likely to be present

Corbett (1907) suggests late planting as a possible means of avoiding the disease. This may do very well where the growing season is long, but in New York State the varieties usually planted require practically all the growing season to properly mature their pods. Since the months of July and August are drier on the average than the other months of the growing season, early-maturing varieties planted at the beginning of July might be less likely to be affected with anthracnose than if planted earlier, as the disease would not have as good an opportunity to develop from affected seeds. There are so many other factors of importance in deciding the time of planting, however, that this one of preventing anthracnose can be given little consideration.

Planting early-maturing varieties

There are years when anthracnose does not become prevalent until the fall rains come on, so that an early-maturing variety would escape infection. A variety of white pea bean known as Early Wonder is recommended by Muncie (1916) to Michigan growers because it ripens from ten to fourteen days earlier than other varieties of this kind, and thus matures before diseases have made serious invasion into the tissue of the pod, with consequent spotting of seed. This bean does not ripen appreciably earlier in New York than does the ordinary Navy Pea.

Spraying

It is interesting to note that even before the discovery of bordeaux mixture, the application of a fungicide to bean pods for the control of anthracnose had been made. Frank (1883 b: 523) found that flowers of sulfur greatly decreases the number of cases of infection but provides no real security against the disease. Scribner (1888: 364) states that under some circumstances applications of solutions of sulfate of iron or of copper may be made, but their use on the fruit cannot be generally recommended because of their poisonous character. He suggests the use of liver of sulfur, one ounce to five gallons of water. Galloway (1889) recommends a very early application of hyposulfite of soda, one ounce to one gallon of water, or of potassium sulfide, one-fourth ounce to one gallon of water. Two subsequent sprayings should be made after the pods are from one-half to two-thirds developed.

Five years after the introduction of bordeaux mixture into the United States, several investigators recommended its use for the control of bean anthracnose. Beach (1892:314–317, 326) experimented with cupric borate, cupric polysulfide, and bordeaux mixture. The last-named was much superior to the others and increased the yield to nearly double that of unsprayed plants. Beach emphasized the importance of spraying thoroughly and of using a nozzle that would produce a misty spray. He believed that the addition to the mixture of enough soap to make suds would cause the mixture to form a thin film over the leaves instead of minute drops. McCarthy (1892:14) recommends either an iron sulfate or a potassium sulfide solution with lime, to which molasses or glue is added as a sticker. He recommends also, as a substitute for the spray solutions, a dust mixture composed either of sulfur flour or precipitated copper carbonate diluted with some dry powdered material, as air-slaked lime or wheat flour. He believes that the application should be made as soon as the flowers have withered if there is any disease in the neighborhood. Halsted (1895 [Halsted and Kelsey] to 1901) carried on spraying experiments with beans for seven years. He used a large number of fungicides, including lime-bordeaux of various strengths, soda-bordeaux, potash-bordeaux, ammoniacal copper carbonate, eau céleste, creolin, and potassium sulfide. Soap also was used in combination with copper sulfate and with eau céleste. Halsted found that there was little difference between the regular bordeaux and the soda-bordeaux in their effects, but the other fungicides proved inferior and creolin was practically worthless. When anthracnose and blight were prevalent they were reduced materially, in most cases, by spraying with bordeaux. With the two successive crops of 1896 (Halsted, 1897:330) and the two of 1897 (Halsted, 1898:310, 312), the check row yielded more beans than did the sprayed rows. During the dry seasons of the year 1900 (Halsted, 1901 b:420, 421), little or no success was obtained from spraying. Whetzel (1906:208) relates an instance in which a single spraying reduced the amount of anthracnose 20 per cent. Blin (1906) obtained relatively good results in France during 1901 and 1902 from spraying with bordeaux. Von Diakonoff (1909) advises bordeaux or a copper-sugar-lime mixture.

County agricultural agents have occasionally reported instances in which spraying has given good results in preventing the disease. Nearly all the spray calendars and bulletins on the subject issued by the various

experiment stations include spraying with bordeaux mixture in their recommendations for control of bean anthracnose. In later years, instances have occurred in which bordeaux was reported as not successful in controlling the disease although the vines were well sprayed.

Fairchild (1894), White (1906:95), Corbett (1907), and Whetzel (1908: 433) question the practicability of spraying beans generally, although granting that there may be circumstances under which it could be recommended. Whetzel has succeeded, however, in controlling the disease on a few rows by thoroughly and properly applying the mixture with a hand machine. He says that the field machines are not constructed so that the mixture can be applied as thoroughly and effectively as by hand. He believes that until a machine is put on the market capable of delivering a spray that will cover the stems and the pods at any stage in the growth of the plant, little or no results can be expected from spraying, and even then the practice will be very expensive because of the machinery, chemicals, and labor involved. Hollman (1915) sprayed plants grown from affected seed with 1-per-cent bordeaux mixture without much success, but he advises its use as a protective measure. Fischer (1919:249) tells of Schander and Krause's experiments at Bromberg, where a 1- or 2-per-cent soda-bordeaux and a 1- or 2-per-cent lime-bordeaux were used. The soda-bordeaux killed the plants and the lime-bordeaux injured them, at least when the solution contained just enough lime to neutralize the copper sulfate solution. Later experiments with 1-per-cent bordeaux, even when seed from healthy pods sorted from diseased plants was used, reduced only slightly the number of affected pods and did not prevent the disease from appearing on the leaves and stems.

The writer conducted spraying experiments during the years 1908 and 1909 in large fields of canning beans at Oneida, New York, in cooperation with the Burt Olney Canning Company, in small experimental plots at Oneida during 1908, 1909, and 1910, and at Ithaca, New York, for six years after 1910. The field sprayings were conducted on 200 acres or more of beans. These were sprayed five times during the growing season, at intervals of about ten days, the applications beginning when the plants were just out of the ground and continuing until after picking had begun. Bordeaux mixture (4–4–50) was used on part of each field and lime-sulfur (1–50) on another part, the two sprayed areas being separated by fifteen unsprayed rows. With the varieties of beans grown, Refugee Wax and

Refugee Green Pod, the pods and the undersides of the leaves, which are the particular points of attack, are so protected by their bushy growth that it is very difficult to apply the mixture thoroughly to these places with the ordinary field sprayer. A Niagara gas sprayer was used and the mixture was delivered at 100 pounds pressure from near the ground to the sides of the plant (fig. 20). Two and sometimes three machines were kept busy during the spraying season. In 1908 the company expended $1000 for bean spraying alone, and in 1909 the expenditure was $1250. Each application cost about $1 an acre. Thus the spraying

FIG. 20. PLATFORM AND APPARATUS FOR PREPARING BORDEAUX MIXTURE IN LARGE QUANTITIES, AND SPRAYING MACHINE DEVISED ESPECIALLY FOR SPRAYING BEANS

question was of sufficient importance to the officials of the company for them to wish to have its value demonstrated, and this in spite of the fact that they had been spraying for the past seven years.

A calculation of the yield, and of the amount of anthracnose and blight, for the three center unsprayed check rows and for the three bordeaux-sprayed rows adjoining, was made at each picking of every field. A calculation of the yield of plants sprayed with lime-sulfur was made from only a few fields.

The amount of anthracnose and of blight during the two years was negligible. The difference in yield between sprayed and unsprayed rows was slight, being one year in favor of the sprayed rows and the following

year in favor of the unsprayed, and in both cases being well within the range of experimental error. The company has since discontinued spraying beans.

During the eight years since 1908 a few rows of beans have been thoroughly sprayed with bordeaux, and a few with lime-sulfur, a hand machine being used. From four to six thorough applications were made throughout the season, beginning soon after the plants appeared and continuing until the pods were about two-thirds grown. The first year neither anthracnose nor blight appeared to any appreciable extent, even on the check rows. In 1909 no anthracnose was present, but the blight appeared to be controlled somewhat by the application of the spray. With one variety, Refugee Green Pod, there was no blight on the sprayed rows while in the unsprayed rows 3 per cent of the pods were spotted with blight. On the Red Marrows that were sprayed 2 per cent of the pods were spotted with blight, while the unsprayed rows had 11 per cent of spotted pods.

In 1910 both anthracnose and blight were again negligible. In 1911, one-third of each of six rows was planted on June 22 to seed of several varieties mixed together, all badly spotted with anthracnose. Mixed varieties were used because it was not possible to obtain a sufficient quantity of affected seed of one variety. The remaining two-thirds of the six rows were planted at the same time to seed selected from clean pods, three rows to Red Marrow and three to Navy Pea. The first and fourth rows were sprayed with bordeaux, the second and fifth rows were not sprayed, and the third and sixth rows were sprayed with lime-sulfur. Powdered arsenate of lead at the rate of 2 pounds to 50 gallons was added to both the bordeaux and the lime-sulfur, in the hope of killing insects that might be instrumental in carrying the blight organism. Five applications were made during the season, on June 13, July 1, 14, and 25, and August 9. One-half of the plants in that part of the plot farthest from the end planted to spotted seed were inoculated with a suspension of spores of two strains of *Colletotrichum lindemuthianum* which had proved virulent on the two varieties. This left one-half of the plants from clean seed as a middle third of each row uninoculated with the fungus in any way except with spores that might be carried to them. Two inoculations were made, one on July 17 when one-half of the plants set aside for this purpose were inoculated, and the other on August 22, when the remainder

were inoculated. These inoculations were made at times when the weather promised exceptionally favorable conditions for infection, and it proved to be so in each case. The plan of the experiment may be outlined as follows:

Application	Clean seed		Spotted seed, plants not inoculated artificially
	Plants inoculated artificially	Plants not inoculated artificially	
Bordeaux I	Red Marrow	Red Marrow	Mixed varieties
Not sprayed I	Red Marrow	Red Marrow	Mixed varieties
Lime-sulfur I	Red Marrow	Red Marrow	Mixed varieties
Bordeaux II	Navy Pea	Navy Pea	Mixed varieties
Not sprayed II	Navy Pea	Navy Pea	Mixed varieties
Lime-sulfur II	Navy Pea	Navy Pea	Mixed varieties

The spotted seed was largely of the wax type, and the pods were picked when a majority were of marketable size as string beans. The results from this experiment are given in table 7. The healthy pods, after being sorted out, were left in a basket for three days. They were then sorted again and the percentage of pods that had spotted in the meantime was

TABLE 7. YIELD, AND PERCENTAGE OF PODS SPOTTED WITH ANTHRACNOSE AND BLIGHT, FROM SPRAYED AND FROM UNSPRAYED ROWS OF SNAP BEANS GROWN FROM SEED BADLY SPOTTED WITH ANTHRACNOSE, IN 1911

Treatment	Date of picking	Number of plants in row	Number of healthy pods	Pods spotted with anthracnose (per cent)	Pods spotted with blight (per cent)	Additional pods spotted with anthracnose after being picked three days (per cent)
Bordeaux I	August 13	62	307	0.6	1.2	0.3
Check I	August 13	71	663	1.7	6.7	20.0
Lime-sulfur I	August 13	62	380	1.8	12.8	0.0
Bordeaux II	August 17	71	722	4.0	0.1	3.3
Check II	August 17	70	557	18.8	4.5	10.7
Lime-sulfur II	August 17	82	592	2.0	1.5	0.5

determined. No importance is attributed to the comparative yield in number of pods given in table 7, as the seed was mixed and more plants of a prolific nature may have been present in one row than in another.

It is seen from table 7 that there was a decided control of the disease by spraying with either bordeaux or lime-sulfur. The control is especially noticeable on pods three days after picking.

The results with field beans grown from healthy seed are given in table 8. It is seen from this table that spraying the vines with either bordeaux or lime-sulfur materially reduced the percentage of spotted pods due to anthracnose. The spraying does not appear to have controlled the blight.

The pods sprayed with bordeaux in the above experiments were decidedly discolored by the precipitate from the mixture. Fawcett (1907) points out that this may be avoided by making the last application with ammoniacal copper carbonate, which leaves no stain. The pods sprayed with lime-sulfur showed no evidence of stain at picking time.

In 1912 complete results from spraying were obtained from only a small plot, two-thirds of which consisted of Red Marrows planted with seed from clean pods while the other third of each row was planted with spotted seed of mixed varieties. The planting was done on June 13, and applications of fungicides were made on July 7, 17, and 26, and August 6. Bordeaux (4–4–50) and lime-sulfur (32° Baumé, 1–50) were the fungicides used. The results are given in table 9. From this table it is seen that no control of anthracnose was obtained from spraying, and that seeds from clean pods were nearly as badly affected as those from spotted seed. Earlier in the season (July 26), however, the plants from clean seed had shown practically no infection, but infection was common on the plants from spotted seed. Cool, rainy weather during August brought about abundant infection from numerous sources.

In 1913 spraying was done on seven varieties planted in eleven plots 50 feet long. Plots 1, 2, and 3 were planted with seed a small percentage of which was spotted with anthracnose; plots 4, 5, 6, 7, 8, and 9 with seed a large percentage of which was similarly spotted; and plots 10 and 11 with seed from selected clean pods. The planting was done on June 29. The Red Valentine and Challenge Black Wax beans did not germinate well and were replanted on July 12. Applications of fungicides were made on July 16 and 26, and August 6 and 16. The Navy Pea and Red Kidney

TABLE 8. YIELD, AND PERCENTAGE OF PODS SPOTTED WITH ANTHRACNOSE AND BLIGHT, FROM SPRAYED AND FROM UNSPRAYED ROWS OF FIELD BEANS GROWN FROM SELECTED HEALTHY SEED, IN 1911

	Variety	Treatment	Number of plants	Yield of dry pods (grams)	Yield of seed (grams)	Pods spotted with anthracnose (per cent)	Pods spotted with blight (per cent)	Clean pods (per cent)	Spotted seed (per cent)
Not inoculated artificially	Red Marrow	Bordeaux.....	52	1,255	806	25.0	6.5	68.5	0.0
		Check.....	58	1,335	947	76.0	0.0	24.0	18.0
		Lime-sulfur...	56	1,045	765	20.0	3.5	76.5	10.0
	Navy Pea	Bordeaux.....	49	936	704	0.0	5.0	95.0	0.0
		Check.....	47	935	715	36.0	11.0	53.0	10.0
		Lime-sulfur...	48	1,115	850	12.0	14.0	74.0	1.0
Inoculated artificially twice during season	Red Marrow	Bordeaux.....	114	2,525	1,830	33.0	5.3	61.4	0.0
		Check.....	118	2,055	1,455	82.0	1.0	17.0	21.0
		Lime-sulfur...	118	2,010	1,452	27.5	5.5	67.0	17.0
	Navy Pea	Bordeaux.....	92	1,575	1,220	4.0	5.5	90.5	1.0
		Check.....	90	1,610	1,215	49.0	4.5	46.5	10.0
		Lime-sulfur...	92	1,675	1,275	24.0	5.0	71.0	3.5

beans, since they would mature later, were given another application on September 8. Bordeaux (5–5–50), Pyrox (1 pound to 5 gallons of water, as recommended on the label), and lime-sulfur (32° Baumé, 1–50), were

TABLE 9. YIELD, AND NUMBER AND PERCENTAGE OF RED MARROW BEAN PODS SPOTTED WITH ANTHRACNOSE, FROM SPRAYED AND FROM UNSPRAYED ROWS IN 1912

Seed planted	Treatment	Number of pods	Pods affected with anthracnose	
			Number	Per cent
Clean seed	Bordeaux	2,600	2,450	93
	Check	1,452	1,450	99
	Lime-sulfur	1,983	1,950	98
Spotted seed	Bordeaux	392	392	100
	Check	227	227	100
	Lime-sulfur	295	295	100

the fungicides used. A killing frost occurred on September 15. Only the percentage of pods spotted with anthracnose is given in table 10, showing the results:

TABLE 10. PERCENTAGE OF PODS SPOTTED WITH ANTHRACNOSE IN SPRAYED AND IN UNSPRAYED ROWS, FROM ELEVEN PLOTS CONTAINING SEVEN VARIETIES OF BEANS, IN 1913

Plot	Variety	Treatment			
		Bordeaux	Pyrox	Not sprayed	Lime-sulfur
1	Red Kidney	0.0	0.0	0.0	0.0
2	Crystal Wax	*2.4	*0.2	*1.4	*1.0
3	Red Valentine	0.0	0.6	0.0	0.0
4	Challenge Black Wax	0.2	0.8	57.2	0.8
5	Navy Pea	0.4	0.4	0.4	0.4
6	Red Kidney	4.6	6.2	58.6	17.4
7	Crystal Wax	0.2	7.0	36.4	20.8
8	Golden Wax	0.0	0.0	0.0	0.0
9	Refugee Wax	0.0	0.0	0.0	0.0
10	Red Kidney	0.0	0.0	0.0	0.0
11	Navy Pea	0.0	0.0	0.0	0.0

* The cotyledons showed anthracnose lesions.

The season was dry and anthracnose was not abundant, but the results on plots 4, 6, and 7, the only ones having a considerable amount of anthracnose in the checks, lead to the conclusion that the fungicides were effective in the following order: bordeaux, Pyrox, lime-sulfur, with the latter falling short somewhat.

Spraying was continued during 1914 on Refugee Wax, Davis Wax, Flageolet Wax, an unidentified wax, and Burpee's Stringless Green Pod. Rows 50 feet long of each variety were planted on June 2, on plots situated side by side on the same land that was used for this purpose in 1913 (table 11). The Flageolet Wax contained a large percentage of seed spotted with anthracnose, but the seed of the other varieties included only a small amount of spotted seed. The row of Flageolet Wax had many missing hills. Applications of the fungicides were made on July 2, 15, and 26, and August 9. One row of each variety was sprayed with bordeaux (5–5–50), one row of each, except the unidentified wax, with Pyrox (1 pound to 5 gallons of water), and one row of each except Flageolet Wax and the unidentified wax with Sulfocide, a commercial sulfur solution (1 gallon to 200 gallons of water). The remaining row of each variety was left unsprayed as a check.

In order to insure anthracnose infection, two inoculations with spores of *Colletotrichum lindemuthianum* obtained from cultures were made, one on August 2 and the other on August 16. Favorable weather for infection followed in each case, and the weather at Ithaca during the summer continued favorable for the development of the pathogene. All the varieties matured their pods before frost and a record of healthy and spotted pods was made on October 8 (tables 11 and 12).

This experiment shows that all the spray materials used had value in the control of anthracnose and blight. The plants from spotted seed were badly affected, and the control of the disease by spraying was not so good on them as on plants from clean seed.

In 1915 but one variety, Davis Wax, was used in the spraying experiment. Two rows 50 feet long were planted on June 8, one to be sprayed and one to be left as a check. One-third of each row was planted with seed of this variety spotted with anthracnose, and the other two-thirds with seed from selected clean pods. A thorough natural inoculation took place, and so it was not necessary to inoculate artificially. The beans

appeared on June 16 and applications of a fungicide were made on June 19, July 3, 10, 24, and 30, and August 7. Pyrox (1 pound to 5 gallons of water) was used for the first three applications and bordeaux 5–5–50

TABLE 11. YIELD, AND NUMBER AND PERCENTAGE OF PODS SPOTTED WITH ANTHRACNOSE AND WITH BLIGHT, IN SPRAYED AND IN UNSPRAYED ROWS IN 1914

Variety	Treatment	Total number of pods	Pods spotted with anthracnose		Pods spotted with blight	
			Number	Per cent	Number	Per cent
Refugee Wax	Bordeaux	1,120	3	0.3	5	0.5
	Pyrox	1,134	10	0.9	3	0.3
	Check	1,467	129	8.8	7	0.5
	Sulfocide	1,307	93	7.1	4	3.1
Davis Wax	Bordeaux	612	33	5.4	12	2.0
	Pyrox	475	19	4.0	11	2.3
	Check	344	23	6.6	59	17.2
	Sulfocide	173	10	5.8	27	15.6
Flageolet Wax	Bordeaux	74	6	8.0	5	6.8
	Pyrox	90	23	25.8	3	3.3
	Check	174	151	86.8	4	2.3
Unidentified wax	Bordeaux	506	20	4.0	5	1.0
	Check	252	46	18.3	13	5.2
Burpee's Stringless Green Pod	Bordeaux	776	76	9.8	10	1.3
	Pyrox	670	40	6.0	9	1.3
	Check	641	131	20.3	28	4.3
	Sulfocide	411	55	13.4	27	6.6

TABLE 12. AVERAGE PERCENTAGE OF PODS SPOTTED WITH ANTHRACNOSE AND WITH BLIGHT FROM THE VARIOUS SPRAYED AND UNSPRAYED PLOTS ON THE RESPECTIVE VARIETIES EMPLOYED, IN 1914

Treatment	Anthracnose (per cent)	Blight (per cent)
Bordeaux	5 5	2.3
Pyrox	9 2	1.8
Check	28 2	5.9
Sulfocide	8.8	5.1

for the other three, the change to bordeaux being made because of the injury resulting to the vines from the use of Pyrox; three hills, in fact, were killed, and the others on July 15 looked very straggling from the loss of their lower leaves, so that they presented a much less satisfactory appearance than the unsprayed rows, even though they were but little affected with anthracnose. The results of this experiment are given in table 13:

TABLE 13. YIELD OF DAVIS WAX BEANS, NUMBER AND PERCENTAGE OF PODS AFFECTED WITH ANTHRACNOSE, AND WEIGHT OF GOOD AND OF CULL SEEDS, FROM SPRAYED AND FROM UNSPRAYED ROWS IN 1915

Seed planted		Sprayed	Not sprayed
Spotted seed	Number of plants	26	30
	Number of pods	122	129
	Number of pods affected with anthracnose	43	129
	Per cent of pods affected	35	100
	Weight of good seed (grams)	79	10
	Weight of cull seed (grams)	17	52
Clean seed	Number of plants	66	86
	Number of pods	240	521
	Number of pods affected with anthracnose	22	521
	Per cent of pods affected	9	100
	Weight of good seed (grams)	290	89
	Weight of cull seed (grams)	49	410
Total	Number of plants	92	116
	Number of pods	362	650
	Number of pods affected with anthracnose	65	650
	Per cent of pods affected	18	100
	Weight of good seed (grams)	369	99
	Weight of cull seed (grams)	66	462

This experiment, although not conducted on an extended scale, shows conclusively the control that can be obtained by spraying the plants thoroughly with bordeaux mixture a sufficient number of times during the season to protect them.

Spraying was continued in 1916 on Davis Wax and Refugee Wax beans. Two rows 40 feet long of each variety were planted on June 10; spotted seed was used in one-third of each row, and healthy seed in the remainder. No artificial inoculations were made. One row of each variety was left

unsprayed as a check, and one of each was sprayed with bordeaux mixture (5 5 50) on July 3, 12, and 24, and August 3, 14, and 24. Data obtained at harvest, October 4, are given in table 14:

TABLE 14. YIELD OF DAVIS WAX AND REFUGEE WAX BEANS, AND NUMBER AND PERCENTAGE OF PODS AFFECTED WITH ANTHRACNOSE, FROM SPRAYED AND FROM UNSPRAYED ROWS IN 1916

Variety	Treatment	Number of plants	Total number of pods	Pods affected with anthracnose		Weight of good seed (grams)	Weight of cull seed (grams)
				Number	Per cent		
Davis Wax	Sprayed.....	59	520	93	18	652	64
	Not sprayed..	61	437	184	42	175	93
Refugee Wax	Sprayed.....	80	770	16	2	370	104
	Not sprayed..	74	662	121	18	.....	.....

It seems to the writer, in view of the results of these experiments, that anthracnose and possibly blight may be kept in check by thoroughly spraying the plants with bordeaux mixture, if the operation is begun soon after the plants have appeared above ground and continued at intervals of about ten days until the pods are reaching marketable size. The nature of the growth of the plants determines to a considerable degree whether they may be sprayed well with a spraying machine. Varieties such as those used in the field experiments at Oneida are so bushy that it is very difficult to spray them thoroughly, while such varieties as Crystal Wax, Currie, Davis, Detroit, Double-Barrel, and others, which have a more erect growth, although compact, are less difficult of such treatment.

The field experiments at Oneida show conclusively that it does not pay to spray during a dry season. Spraying experiments conducted on a small scale with hand sprayers have shown that it is possible to control the disease to a considerable extent by this method. Whether the disease can be controlled as well with traction or power machines during epiphytotic years is yet an unsettled question.

In regions where anthracnose usually occurs annually, spraying can probably be used to advantage if the practice is supplemented by the use of clean seed. In New York spraying is not practicable for growers of dry beans, and probably not for growers of canning beans. If the total cost of making five applications is $7.50 an acre, it would be necessary for growers of dry beans to get from spraying an increase of 1.5 bushels an acre each year with beans selling at $5 a bushel in order to balance accounts. A decided increase in yield could be expected in a year when anthracnose was prevalent, but none if the season were dry. If an epiphytotic of the disease occurs in two out of seven years, as was the case from 1908 to 1915, then it would be necessary for the grower to get an increase from spraying of about 5.25 bushels in each of such two years in order to come out even. In order to make spraying pay, he must get a greater increase in yield or the selling price must be greater, and the time spent in spraying must not be at the expense of other farm operations.

Applying a fungicide to picked pods before shipping

Rolfs (1897) recommends the application of a sulfur spray just before packing pods for shipping, in order to kill the spores adhering to the pods. Fawcett (1907) also recommends the application of either potassium sulfide or a soda-sulfur spray. He says the pods should be spread out on the floor and the spraying solution thoroughly applied, the pods being turned over during the operation so that all the surfaces will be covered. The pods should be allowed to dry before being crated. In order to guard further against infection, Kirk (1905) suggests the exclusion of affected pods in packing, and Fulton (1908:12) says that affected pods should not be picked, washed, nor packed with sound ones. Containers should be so devised as to allow good ventilation, and the pods should be stored in as dry and cool places as is possible. Since there will be no anthracnose infection on pods during shipment if the disease is controlled in the field, stress should be placed on such control.

Application of a fungicide to the soil

Halsted (1900 a:380) is the only investigator who has ever recorded the application of any fungicide to the soil in an effort to control bean anthracnose, and in his experiment there was no anthracnose on any of his bean

plants throughout the season although blight was present to some extent. He applied bordeaux mixture to the soil at the rate of 4320 gallons to the acre. In the first crop of the year the blight was reduced one-half on leaves and pods, but in the second crop there was just as much blight on these plants as there was on the check. Moreover, the plants growing on land that had received the application were smaller than those on the untreated soil.

Rotation of crops

The idea that the fungus is able to winter in the soil has led many writers to recommend, among other suggestions, that the grower should not plant beans on land that bore a diseased crop the previous season. Harvey (1894: 153) calls attention to this, and in the same year Cobb (1894) advises a change of ground. Halsted (1900 b: 127), after growing beans each year on the same ground for a number of successive years, found that the plants yielded more in the first four years than when grown on new land, but less afterward. Usually a greater number of spotted pods were produced on plants grown year after year on the same land.

Observations were made by the writer on beans grown as the seventh successive crop on the same land. They appeared as thrifty, and yielded as well, as any crop grown on rotated land. Moreover, they were as free from anthracnose and blight as the others, although in fairness it must be said that the summers had been dry for the three years preceding the observations. There is little chance of anthracnose occurring where beans are planted year after year on the same ground, if the vines, when affected, are not returned to this soil. There is greater danger that such a practice will introduce other diseases, especially stem rots, which tend to reduce the yield materially.

Selection of resistant plants

As has been stated earlier in this paper (page 149), no variety of *Phaseolus vulgaris* has been found to be absolutely immune to anthracnose, although a selection of the ordinary Red Kidney has been obtained which has proved to be resistant to such an extent that it will produce a very satisfactory yield in years when the ordinary Red Kidney becomes badly affected, and a Nova Scotia White Marrow has been located that shows considerable resistance in the field although susceptible in the seedling stage when inoculated artificially. Further progress in obtaining resistant

beans with these as a basis for hybridization is being made, the resistance being readily tested by artificial inoculation in the field, the cold frame, or the green-house. Selections can be made of large numbers of individuals by artificially inoculating them while in the seedling stage. Any showing marked resistance can be allowed to mature seed, and further tests can be made with them. Investigators are beginning to realize that the selection of plants resistant to disease is a most practical and satisfactory method of disease control, and even now work of this kind is engaging the attention of phytopathologists to a very marked degree.

As already stated (page 149), there are many varieties of beans which, while susceptible to one strain of the pathogene, are resistant to the other. It has been observed that often only one variety of beans is grown in a given locality; for example, Shepard (1919) reports that in 1918 pea beans constituted 76 per cent of all beans grown in Orleans County and 77 per cent of all grown in Monroe County, while in Yates County only 6 per cent of all beans are pea beans while 30 per cent are White Marrow, 29 per cent are Yellow Eye, and 15 per cent are Red Kidney. It happens that the pea bean referred to is susceptible to strain *alpha* of the pathogene but resistant to strain *beta*, while the other varieties mentioned are susceptible to strain *beta* but resistant to strain *alpha*. It is very likely that in regions where the pea bean is grown, strain *beta* does not exist to any great extent, and the introduction of clean seed of varieties resistant to this strain, even if susceptible to the other, would give crops of these varieties free from anthracnose for a few years. Eventually the *beta* strain would appear, and, its host being prevalent, would develop abundantly in years favorable for it. Similar results could be expected from the introduction of the pea bean, or any other variety resistant to the *beta* strain, into localities where this strain is the only one prevalent. There are other factors, to be sure, which tend to discourage a change in varieties in a given locality, and these have largely operated to prevent such changes.

Consideration of prophylactic measures

Bean anthracnose occurs to a serious extent in New York only during two or more wet seasons in succession, and the losses occasioned at such times are often forgotten by the grower in the dry seasons that intervene. It is a question with him then whether the time and the money needed for

successful control measures would not be lost in carrying them out. At the time when the disease occurs, however, he is willing to do anything to lessen its destructiveness. With bean anthracnose, as with most other plant diseases, control measures to be successful must be given consideration before the disease appears, or, better, before the crop is planted; and whatever measures are decided upon must be carried out completely. Frantic attempts to control the disease after it has appeared are usually a waste of time and money and cannot be generally recommended.

When one considers the various measures suggested for the control of this disease, he must realize that each has disadvantages and that the cost would be greater than the gain were all carried out even though the disease was thereby controlled. Some measures offer a greater promise of success than others. These are here summarized and briefly discussed.

Seed disinfection may prove to be worth while, but more experimental work is necessary before it can be recommended.

The avoidance of conditions favorable to the fungus is a precautionary measure that should receive consideration from all bean growers since it involves little or no expense.

Spraying is not a practicable measure for growers of dry beans in New York, but frequent and thorough applications of bordeaux mixture can be depended on to protect the plants from anthracnose; and such a control measure is practicable when the value of the crop is sufficiently great to warrant the expense involved.

As far as present evidence indicates, the application of a fungicide to the soil is impracticable and ineffective.

Rotation of crops, in itself, will not prevent anthracnose nor reduce the liability of its occurrence to any marked extent; but it is a measure that should receive some consideration, since its practice may serve to keep down the losses occasioned by other diseases.

The disinfection of picked pods need be considered only by growers of snap beans who ship to distant markets. This will not be necessary for growers who are successful in controlling the disease in their fields.

The use of anthracnose-resistant varieties is a satisfactory means of control and should be taken advantage of when possible.

The practice of careful hand-picking in order to remove diseased seed cannot be depended upon as an effective control measure because affected seed will escape the eye of the most practiced observer. However, this

practice will reduce the amount of affected seed planted, and if the seed is picked over at least twice the chances of getting a clean crop will be greatly improved as compared with the use of seed that has not been carefully hand-picked.

SUMMARY

Bean anthracnose is a disease of beans, principally affecting varieties of *Phaseolus vulgaris* L., which was first definitely reported and described in 1878 although it probably existed at a much earlier date. It has since been reported from every continent, and from nearly every country where beans are grown.

The disease has caused very large losses in years favorable for its development. In the eastern part of the United States, epiphytotics have occurred in the years 1906 to 1908 and 1914 to 1917.

All parts of the plant, even the roots, are subject to the disease, but it is most noticeable on the pods, where it forms dark, sunken cankers which subsequently extend to the seed contained within.

The spores germinate readily at room temperatures, within twenty-four hours in nutrient culture media and in bean agar and more slowly in water, the germ tube usually forming an appressorium on contact with a hard substratum.

A moderate growth of mycelium is produced in culture, which becomes dark-colored and forms acervuli from which a flesh-colored mass of spores is exuded. Under favorable conditions spores may be produced after three days growth. Cultures lose their power to produce spores by age or continued exposure to temperatures above the optimum. As the culture dries, setae are produced within and around the acervuli.

The minimum temperature for growth lies between 0° and 4° C., the optimum near 22°, and the maximum between 34° and a few degrees lower.

The fungus after entering the host extends its hyphae horizontally and diagonally into the cells. Browning of the cell contents occurs soon after the attack. The walls collapse and a lesion may be observed, at the earliest, four and one-half days after inoculation.

A stroma is formed at about the time when the cells collapse, and from it arise, in various places, a cluster of conidiophores which push up the epidermis, forming pimples. Spores are produced at the extremity of

the conidiophores, and these spores break through to the surface as a pasty mass. The fungus is capable of living from one season to another, and even for two seasons, in old affected vines and pods, which may serve as a source of inoculum when carried to the field. Spores washed into the soil are not viable to any extent after seven weeks.

The fungus when it invades the seed is able to live in its tissues in a more or less inactive condition for at least two years when the conditions of seed storage are not unfavorable for it.

Plants in the seedling stage and the youngest parts of older plants are the most susceptible to the disease.

There are at least two strains or biologic forms of the fungus. Many varieties of *Phaseolus vulgaris* resistant to the one are susceptible to the other, and vice versa. There are some varieties that are very susceptible to both strains, and at least one that is highly resistant to both. The wax-podded bush beans include a larger percentage susceptible to both strains than are found in other groups of varieties.

Several other species of Phaseolus are susceptible to anthracnose, but in this country, with rare exceptions, the disease is not severe nor often noticeable on such plants.

A few species of the related genera Vigna (cowpea) and Dolichos (kulthi and val bean) have shown some susceptibility in a few cases, but plants of other genera which have been inoculated have shown complete immunity.

Varieties of *Phaseolus vulgaris* are not susceptible to infection by fungi causing anthracnose of other plants, so far as infection experiments on them have been tried.

Selection of seed from clean pods has given a crop free from anthracnose in nearly all cases, and has always given anthracnose-free seedlings in clean soil.

Western-grown bean seed gave crops free from anthracnose but with considerable blight.

Spraying with bordeaux mixture throughout the season has prevented anthracnose to a large extent even in seasons favorable for it. In dry seasons spraying does not increase the yield. Applications of lime-sulfur solution and of two prepared fungicides gave some control, but not as good control as did bordeaux mixture.

The use of resistant varieties gave greatest promise of a satisfactory means of control.

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PLATE I

PATHOLOGICAL ANATOMY OF BEAN ANTHRACNOSE

1, Section across an anthracnose lesion on an immature pod, showing depth of lesion, affected tissues, and spore masses. Drawn with aid of camera lucida. × 25

2, Section across a lesion on pod of Golden Refugee bean, showing an acervulus with spores and several setae. Drawn with aid of camera lucida. × 166

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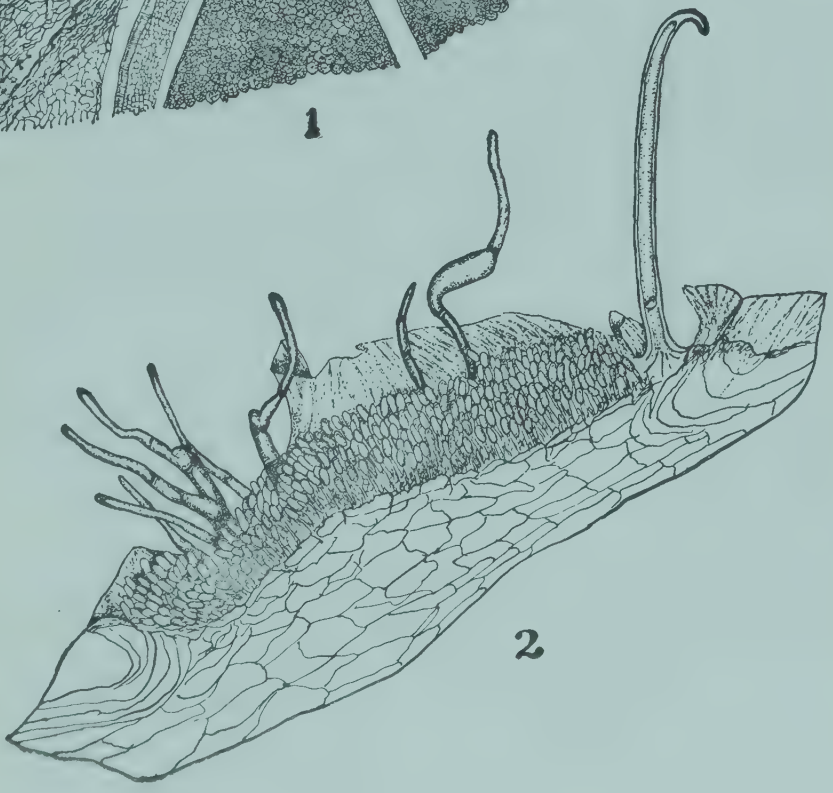

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PLATE II

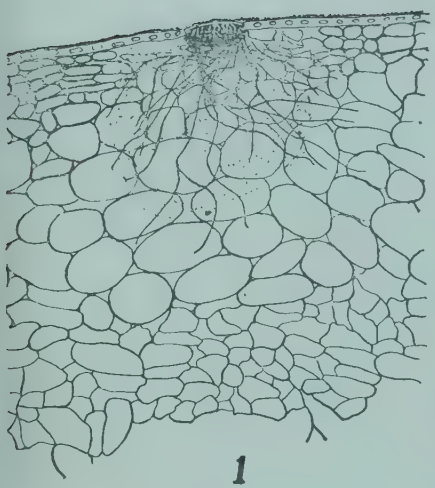
DEVELOPMENT OF COLLETOTRICHUM LINDEMUTHIANUM WITHIN HOST TISSUE

1, Section across very small, newly formed lesion on Refugee Wax bean pod. The dotted part represents discolored area as seen in the microscope, the mycelium extending beyond this. Spores are being produced in a pocket beneath the cuticle, which is not yet ruptured. × 55

2, Same tissue, higher magnification. The disorganization of subepidermal cells can be noted. × 166

3, A few cells from cross section of an infected wax-bean pod, showing advancing fungous hyphae

4, Section across recently invaded tissue of outer coat of affected pod, showing twelve fungous hyphae penetrating the wall of a cell. × 333



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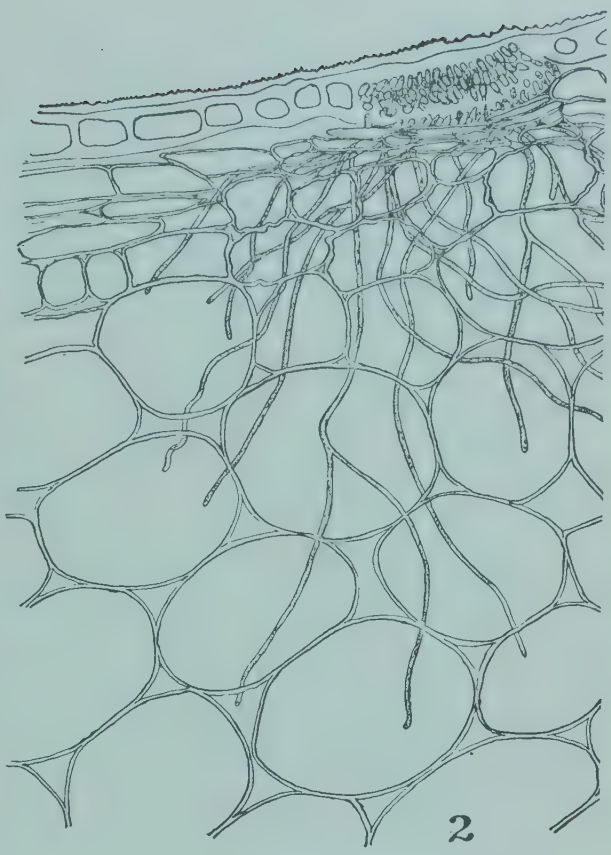

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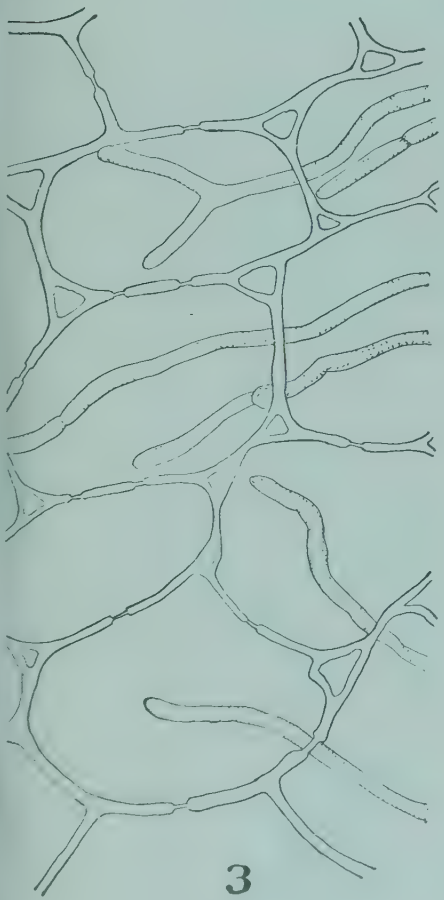

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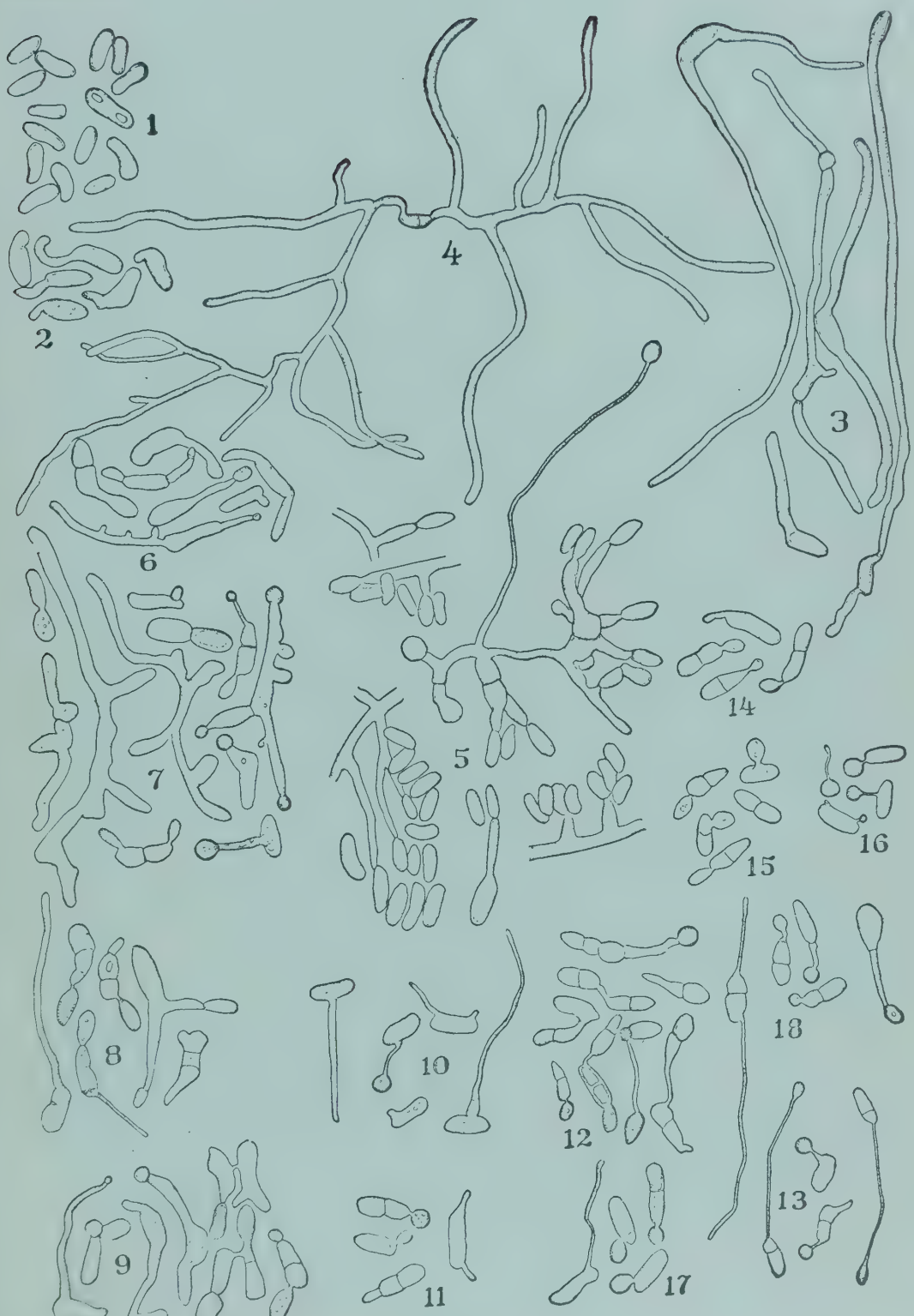
PLATE III

CONIDIA OF COLLETOTRICHUM LINDEMUTHIANUM

(Temperature varied from 20 to 24° C.)

1, Conidia from an acervulus, × 342. 2, Conidia germinating after 9 hours in bean agar, × 339.47. 3, Germination after 20 hours in bean agar, × 347.36. 4, Germination after 54 hours in agar, × 166.73. 5, Spore formation after growth of 4 days in agar, × 347.36. 6, Germination and production of appressoria after 19 hours in sugar solution, × 339.47. 7, After 36 hours in sugar solution, × 347.36. 8, After 66 hours in sugar solution, × 347.36. 9, After 84 hours in sugar solution, × 363.15. 10, After 18 hours in water, × 347.36. 11, After 37 hours in well water, × 363.15. 12, After 65 hours in well water, × 347.36. 13, After 9 days in well water, × 363.15. 14, After 36 hours in distilled water, × 363.15. 15, After 62 hours in distilled water, × 363.15. 16, After 8½ days in distilled water, × 363.15. 17, After 38 hours in rain water, × 363.15. 18, After 66 hours in rain water, × 347.36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ANTHRACNOSE ON BEAN SEEDS

Upper left, Navy Pea; upper right, Red Kidney; lower left, White Marrow; lower right, Brockton.

ANTHRACNOSE ON PODS OF WAX AND GREEN-POD BEANS
The acervuli can be seen in the larger lesions

BACTERIAL BLIGHT ON RED KIDNEY BEAN PODS

RUST (UROMYCES APPENDICULATUS,) ON BEAN PODS

JULY, 1921 MEMOIR 43

CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

VARIATIONS IN BACTERIA COUNTS FROM MILK AS AFFECTED BY MEDIA AND INCUBATION TEMPERATURE

G. C. SUPPLEE, W. A. WHITING, AND P. A. DOWNS

ITHACA, NEW YORK
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G. C. Supplee[1], W. A. Whiting, and P. A. Downs

The increasing importance of the liquid-milk supply for large centers of population and the greater demand for a better quality of raw material for manufacturing purposes have necessitated further knowledge of the methods used in determining the quality of milk, and particularly have emphasized the significance of bacteriological analyses.

Examination of milk for the purpose of determining numbers or types of bacteria seems to constitute the highest ideal in milk grading. This aspect is doubtless important and the respect for this method of procedure in judging milk quality should not be endangered. Obviously, the sanitary aspects of the milk problem must involve determinations of this kind. The significance of bacteria in the economic phases of the milk supply also becomes quite clear when it is remembered that the entire business of supplying milk to the urban population is founded on modern dairy science, of which the aims are maximum wholesomeness and maximum keeping quality. These two considerations have been responsible for the stress laid on the importance of bacteria counts in the milk industry at the present time.

That the methods of enumerating bacteria in milk have many shortcomings is well recognized by dairy bacteriologists. Bacteria counts, as now obtained, can be interpreted only on a comparative basis, and in no sense do they indicate the mathematical accuracy which their expression in numbers implies. Such comparative interpretations can be used only as indications of degrees of success in handling and of the variations of keeping quality. Undeniably this information is valuable in safeguarding the interests of consumers of milk in large cities, and its importance is shown by the report of the Committee on Statistics of Milk and Cream Regulations of the Official Dairy Instructors' Association (1917).[2] This committee obtained the complete milk regulations from 409 cities and

[1]At present Director of Research Department of the Dry Milk Company, New York.
[2]Dates in parentheses refer to *Literature Cited*, page 247.

towns in the United States, and found that 189 of these provided for a legal limit for bacteria in milk sold within the municipality. The limits allowed by these cities ranged from 50,000 to 5,000,000 to the cubic centimeter, with approximately one-half of the cities permitting a limit of 500,000. The necessity of fixing legal limits for bacteria in cream seems to have been regarded as much less important, since only 30 of the 409 cities had established legal limits for this product. The bacteria allowed in the latter case varied from 50,000 to 1,000,000 to the cubic centimeter.

These municipal regulations must of necessity imply provisions for their enforcement and for penalties for failures in their observance. Such provisions immediately bring into prominence the difficulty of application and enforcement of numerical bacterial standards. Unfortunately, the inherent inaccuracies of present methods of enumerating bacteria are too great to permit their results to be relied upon with the certainty of exactness which their fixed numerical standards would seem to warrant.

REVIEW OF PREVIOUS INVESTIGATIONS

The American Public Health Association (1915), recognizing the wide variations obtained by the ordinary, plating technique, have formulated, through their Laboratory Section, the following uniform method for determining bacteria in milk. This procedure, known as the "Standard Methods of Bacterial Analyses of Milk," has been of considerable value in securing uniform technique in different laboratories, and the results are comparable, since a uniform interpretation can be given to them. That the purpose of the Standard Methods is for securing uniform results rather than accurate counts, in the minimum length of time, is evident from the fact that 37° C. for forty-eight hours on plain agar is the only incubation temperature and medium recognized. In the routine examination of milk samples, the short incubation period has certain distinct advantages.

Conn (1915) compiled the results obtained from an exhaustive series of comparative determinations made from the same milk by four laboratories. This work, involving many thousand platings made under uniform procedure, nevertheless failed to give uniform and consistent results under those particular conditions. Viewed from the standpoint of absolutely accurate determinations of all bacteria present, there are numerous

reasons why the plate method gives widely discrepant results. Among the most important causes are: (1) the failure of certain species to produce visible colonies on the medium and in the incubation temperature used; (2) the tendency of many species to exist in groups of two or more individuals, which groups are broken apart with varying degrees of completeness during the plating operation; (3) too few or too many colonies to the plate; (4) the inhibiting or beneficial effect of diffused by-products from the growth of certain species on other species within the radius of diffusion; (5) the personal element involved in carrying out the method. Widely varying results from the same sample of milk under the same conditions of incubation temperature and medium would still be caused by the clumping tendency, by the number of colonies on each plate, and by the personal element entering into the manipulations.

Hill and Ellms (1897) early called attention to the unreliable results obtained from over-crowded plates used in water analysis. The Standard Methods stipulate that there shall be not less than 30, and not more than 200, colonies to the plate, altho Breed and Dotterrer (1916) conclude that limits of 30 and 400 are nearly as satisfactory.

Altho the Standard Methods call for plain agar incubated at 37° C. for forty-eight hours, comparative counts published from time to time have shown that a carbohydrate medium and a longer incubation period at a lower temperature have many advantages. Heinemann and Glenn (1908), from their work on the effect of incubation temperatures and media, reached the following conclusions:

1. Since pathogenic bacteria are always difficult, and in most cases impossible, to find in milk, a high temperature of incubation has no advantage over room temperature from this viewpoint.

2. Incubation at 20° C. is superior to incubation at 37° C. because both a higher count and a better differential count are obtained.

3. Dextrose is preferable to lactose as an addition to the medium.

4. Milk is usually consumed before the results of bacterial examinations are available. Accordingly bacteriological and chemical examinations should have as their principal objects the improvement and control of the general supply; and accuracy being of greater importance than quick results, the loss of a day in its interest is irrelevant.

Sherman (1916) points out the higher counts obtainable by the use of lactose agar in place of plain agar, and also the increase in the size of the colonies and the better differentiation of the types.

Breed and Stocking (1917) published a preliminary report on a series of comparative determinations, in which they conclude that the plate method, when used by careful workers, will give more reliable results than those reported by Conn, which had been obtained under routine conditions and possibly, in some instances, by inexperienced operators. Obviously, inexperience and carelessness are factors to be avoided in any method of enumerating bacteria, especially when the results are for the determination of municipal regulations. The same authors (1920), reporting a similar but more extensive investigation, found the plate method and the microscopic method (Breed method) productive of reasonably uniform and accurate results for the total number of bacteria present, all factors known to introduce inaccuracies having been first reduced to a minimum. For the plate method they report an average coefficient of variability of 8.3; for the microscopic determination of groups of bacteria, consisting of one or more individuals, 11.7; and for the microscopic determination of individual bacteria, 13.4. Altho these results are remarkably uniform, it must be remembered that they are obtained from samples which were artificially inoculated in order to reduce the clumping tendency to a minimum, and that the time and labor necessary to obtain this degree of accuracy by the microscopic method could not be expected in regular, routine examinations.

PRESENT EXPERIMENTS

Comparison of media and incubation temperatures

The experimental work reported herein was for the purpose of demonstrating the variations in counts obtained by plain and carbohydrate media at different incubation temperatures. It may indicate a further reason why the count at 37° C. for forty-eight hours, as used in routine work, may be more subject to discrepancies than counts obtained from longer incubation periods at lower temperatures.

The samples used for this work were selected at random from the ordinary market milk of the Ithaca city supply, at intervals extending over a period of one and one-half years. Twenty-seven plates were made from the same dilution of each sample. Nine of the plates were

poured with standard plain agar; nine with nutrient agar containing 1 per cent of dextrose; and nine with nutrient agar containing 1 per cent of lactose. The different agars were all made from single, large-quantity batches of plain, nutrient agar. These were subdivided, and the definite percentage of the particular carbohydrate desired was added to each. Three of the nine plates containing the different agars were incubated at 37° C. for forty-eight hours; three at 30° C. for five days; and three at 20° C. for five days. With the exceptions noted, the technique given in the Standard Methods was carefully followed. It was necessary, however, to include counts from plates containing fewer than 30 colonies and more than 200 colonies, altho in all cases the dilution was designed to give colonies between these limits from the forty-eight hour count at 37°.

In table 1 are shown the counts obtained from 100 different samples of milk from each of the nine combinations of incubation temperatures and media. The individual counts appearing in this table are the averages of triplicate plates. Each plate of the series of three checked with the other plates of the series as closely as would be expected from duplicate or triplicate plates from the same dilution of any sample of normal milk. In order to indicate in a comprehensive manner the variations obtained, the 37° count was taken as the standard. Any variation above or below this count is indicated by a plus or a minus sign. The variations are shown also as percentages, the 37° count being accepted as 100 per cent, and counts higher or lower being indicated by figures above or below 100.

TABLE 1. Variations in Counts Obtained by Plain and Carbohydrate Agar at Different Incubation Temperatures

Sample	Temperature (C.)	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
1	37°	6,800,000	.....	100	11,610,000	4,810,000+	170	11,940,000	5,140,000+	173
	30°	7,080,000	280,000+	104	11,790,000	4,990,000+	173	10,580,000	3,780,000+	156
	20°	5,970,000	830,000—	88	7,550,000	750,000+	111	10,090,000	3,290,000+	148
2	37°	41,000	.....	100	26,400	14,600—	65	36,600	4,400—	89
	30°	41,300	300+	101	38,400	2,600—	93	38,600	2,400—	94
	20°	41,500	500+	101	34,600	6,400—	85	38,300	2,700—	93
3	37°	17,100	.....	100	16,000	1,100—	93	16,100	1,000—	94
	30°	21,200	4,100+	124	17,000	100—	99	18,800	1,700+	110
	20°	23,100	6,000+	135	18,700	1,600+	109	16,700	400—	98
4	37°	10,300	.....	100	7,100	3,200—	69	9,300	1,000—	90
	30°	14,900	4,600+	145	14,000	3,700+	136	13,100	2,800+	127
	20°	14,400	4,100+	140	12,500	2,200+	121	14,300	4,000+	139
5	37°	710,000	.....	100	440,000	270,000—	62	370,000	340,000—	52
	30°	980,000	270,000+	138	840,000	130,000+	118	770,000	60,000+	108
	20°	920,000	210,000+	130	970,000	260,000+	137	1,060,000	350,000+	149
6	37°	14,100	.....	100	14,500	400+	103	15,900	1,800+	113
	30°	18,600	4,500+	132	15,900	1,800+	113	16,300	2,200+	114
	20°	18,000	3,900+	128	15,700	1,600+	111	16,100	2,000+	116
7	37°	2,400,000	.....	100	1,740,000	660,000—	72	2,290,000	110,000—	97
	30°	2,950,000	550,000+	123	3,150,000	750,000+	131	3,190,000	790,000+	133
	20°	3,060,000	660,000+	127	3,120,000	720,000+	130	2,960,000	560,000+	123
8	37°	11,800	.....	100	18,100	6,300+	153	18,300	6,500+	155
	30°	41,700	29,900+	353	37,800	26,000+	320	36,200	24,400+	307
	20°	39,600	27,800+	336	35,600	23,800+	302	35,700	23,900+	303

9.....	37°	26,600	.....	100	35,400	8,800+	133	26,200	400—	99
	30°	30,300	3,700+	114	29,600	3,000+	111	25,300	1,300—	95
	20°	36,300	9,700+	136	27,500	900+	103	23,600	3,000—	89
10.....	37°	6,270,000	.....	100	5,490,000	780,000—	88	5,970,000	300,000—	95
	30°	5,050,000	1,220,000—	80	6,380,000	110,000+	102	7,060,000	790,000+	113
	20°	7,750,000	1,480,000+	124	6,340,000	70,000+	101	6,430,000	160,000+	103
11.....	37°	116,700	.....	100	122,100	5,400+	105	109,000	7,700—	93
	30°	110,800	5,900—	95	89,600	27,100—	77	107,500	9,200—	92
	20°	96,800	19,900—	83	80,400	36,300—	69	82,800	33,900	71
12.....	37°	1,650,000	.....	100	1,790,000	140,000+	108	1,480,000	170,000—	90
	30°	2,520,000	870,000+	153	2,260,000	610,000+	137	2,290,000	640,000+	139
	20°	2,310,000	660,000+	140	2,310,000	660,000+	140	2,220,000	570,000+	135
13.....	37°	32,000	.....	100	28,800	3,200—	90	31,600	400—	99
	30°	29,400	2,600—	93	36,200	4,200+	113	37,700	5,700+	118
	20°	42,100	10,100+	131	33,500	1,500+	105	35,700	3,700+	112
14.....	37°	830,000	.....	100	780,000	50,000—	94	860,000	30,000+	104
	30°	1,090,000	260,000+	131	960,000	130,000+	116	1,290,000	460,000+	155
	20°	1,150,000	320,000+	139	930,000	100,000+	112	1,190,000	360,000+	143
15.....	37°	278,000	.....	100	274,000	4,000—	99	307,000	29,000+	110
	30°	309,000	31,000+	111	256,000	22,000—	92	282,000	4,000+	101
	20°	324,000	46,000+	117	264,000	14,000—	95	268,000	10,000—	96
16.....	37°	8,500,000	.....	100	7,900,000	600,000—	93	8,400,000	100,000—	99
	30°	10,400,000	1,900,000+	122	8,700,000	200,000+	102	11,900,000	3,400,000+	140
	20°	9,600,000	1,100,000+	113	9,500,000	1,000,000+	112	10,400,000	1,900,000+	122
17.....	37°	12,000	.....	100	11,900	100—	99	10,100	1,900—	84
	30°	12,900	900+	107	10,800	1,200—	90	11,300	700—	94
	20°	10,700	1,300—	90	11,600	400—	97	11,600	400—	97

TABLE 1 (*continued*)

Sample	Temperature (C.)	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
18.....	37°	960,000	.....	100	1,280,000	320,000+	133	990,000	30,000+	103
	30°	1,100,000	140,000+	115	1,220,000	260,000+	127	1,240,000	280,000+	129
	20°	1,090,000	130,000+	114	1,390,000	430,000+	145	1,240,000	280,000+	129
19.....	37°	154,800	.....	100	135,600	19,200—	88	148,100	6,700—	96
	30°	185,400	30,600+	120	142,600	12,200—	92	120,300	34,500—	78
	20°	182,600	27,800+	118	122,800	32,000—	79	178,700	23,900+	115
20.....	37°	660,000	.....	100	660,000	.....	100	810,000	150,000+	123
	30°	720,000	60,000+	109	600,000	60,000—	91	820,000	160,000+	124
	20°	870,000	210,000+	132	800,000	140,000+	121	860,000	200,000+	130
21.....	37°	2,100	.....	100	2,500	400+	119	2,200	100+	105
	30°	2,600	500+	124	2,100	.....	100	2,400	300+	113
	20°	2,500	400+	119	2,700	600+	129	3,400	1,300+	162
22.....	37°	8,000	.....	100	12,000	4,000+	150	18,000	10,000+	225
	30°	34,000	26,000+	425	32,000	24,000+	400	35,000	27,000+	437
	20°	16,000	8,000+	200	32,000	24,000+	400	36,000	28,000+	450
23.....	37°	2,000	.....	100	3,000	1,000+	150	1,000	1,000—	50
	30°	6,000	4,000+	300	2,000	.....	100	3,000	1,000+	150
	20°	4,000	2,000+	200	4,000	2,000+	200	1,000	1,000—	50
24.....	37°	73,000	.....	100	59,000	14,000—	81	35,000	38,000—	48
	30°	76,000	3,000+	104	93,000	20,000+	128	66,000	7,000—	90
	20°	29,000	44,000—	40	11,000	62,000—	15	15,000	58,000—	20
25.....	37°	1,200,000	.....	100	1,687,000	487,000+	140	1,150,000	50,000—	96
	30°	2,281,000	1,081,000+	190	2,304,000	1,104,000+	192	1,181,000	19,000—	98
	20°	325,000	875,000—	27	19,000	1,181,000—	2	2,003,000	803,000+	167

26.....	37°	72,000	.....	100	747,000	675,000+	1,037	1,290,000	1,218,000+	1,792
	30°	70,000	2,000—	98	651,000	579,000+	904	1,478,000	1,406,000+	2,052
	20°	62,000	10,000—	87	31,000	41,000—	43	21,000	51,000—	30
27.....	37°	60,000	.....	100	42,000	18,000—	30	47,000	13,000—	78
	30°	387,000	327,000+	645	371,000	311,000+	618	341,000	281,000+	568
	20°	358,000	298,000+	597	502,000	442,000+	837	345,000	285,000+	575
28.....	37°	80,000	.....	100	76,000	4,000—	95	105,000	25,000+	131
	30°	134,000	54,000+	167	125,000	45,000+	156	130,000	50,000+	162
	20°	127,000	47,000+	159	98,000	18,000+	122	151,000	71,000+	189
29.....	37°	102,000	.....	100	164,000	62,000+	161	243,000	141,000+	238
	30°	160,000	58,000+	157	174,000	72,000+	171	210,000	108,000+	206
	20°	215,000	113,000+	211	184,000	82,000+	180	175,000	73,000+	171
30.....	37°	3,950,000	.....	100	3,290,000	660,000—	84	2,860,000	1,090,000—	72
	30°	6,740,000	2,790,000+	170	6,280,000	2,330,000+	159	4,170,000	220,000+	105
	20°	7,260,000	3,310,000+	184	6,460,000	2,510,000+	163	650,000	3,300,000—	16
31.....	37°	520,000	.....	100	670,000	150,000+	129	1,050,000	530,000+	202
	30°	1,980,000	1,460,000+	381	1,800,000	1,280,000+	346	2,780,000	2,260,000+	534
	20°	1,680,000	1,160,000+	323	1,680,000	1,160,000+	323	1,660,000	1,140,000+	319
32.....	37°	250,000	.....	100	170,000	80,000—	68	350,000	100,000+	140
	30°	580,000	330,000+	232	630,000	380,000+	252	520,000	270,000+	208
	20°	630,000	380,000+	252	520,000	270,000+	208	410,000	160,000+	164
33.....	37°	19,000	.....	100	16,000	3,000—	84	4,000	15,000—	21
	30°	39,000	20,000+	205	43,000	24,000+	226	30,000	11,000+	158
	20°	36,000	17,000+	189	27,000	8,000+	142	28,000	9,000+	147
34.....	37°	80,000	.....	100	98,000	18,000+	122	74,000	6,000—	92
	30°	114,000	34,000+	142	122,000	42,000+	152	110,000	30,000+	137
	20°	85,000	5,000+	106	123,000	43,000+	154	97,000	17,000+	121

TABLE 1 (*continued*)

Sample	Temperature (C.)	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
35.....	37°	106,300	.....	100	125,200	18,900+	118	131,300	25,000+	124
	30°	138,100	31,800+	130	145,200	38,900+	137	114,900	8,600+	107
	20°	133,100	26,800+	125	116,400	10,000+	109	94,900	11,400—	89
36.....	37°	30,000	.....	100	390,000	360,000+	1,300	240,000	210,000+	800
	30°	90,000	60,000+	300	40,000	10,000+	133	620,000	590,000+	2,067
	20°	60,000	30,000+	200	30,000	.....	100	320,000	290,000+	1,067
37.....	37°	10,000	.....	100	10,000	.....	100	70,000	60,000+	700
	30°	50,000	40,000+	500	10,000	.....	100	800,000	790,000+	8,000
	20°	40,000	30,000+	400	30,000	20,000+	300	610,000	600,000+	6,100
38.....	37°	20,000	.....	100	20,000	.....	100	270,000	250,000+	1,350
	30°	30,000	10,000+	150	20,000	.....	100	590,000	570,000+	2,950
	20°	30,000	10,000+	150	30,000	10,000+	150	380,000	360,000+	1,900
39.....	37°	20,000	.....	100	40,000	20,000+	200	140,000	120,000+	700
	30°	60,000	40,000+	300	20,000	.....	100	260,000	240,000+	1,300
	20°	20,000	.....	100	40,000	20,000+	200	300 000	280,000+	1,500
40.....	37°	10,000	.....	100	10,000	.....	100	60,000	50,000+	600
	30°	10,000	.....	100	10,000	.....	100	650,000	640,000+	6,500
	20°	10,000	.....	100	10,000	.....	100	40,000	30,000+	400
41.....	37°	20,000	.....	100	20,000	.....	100	150,000	130,000+	750
	30°	30,000	10,000+	150	20,000	.....	100	190,000	170,000+	950
	20°	10,000	10,000—	50	20,000	.....	100	19,000	1,000—	95
42.....	37°	510,000	.....	100	250,000	260,000—	49	420,000	90,000—	83
	30°	480,000	30,000—	94	550,000	40,000+	107	650,000	140,000+	127
	20°	480,000	30,000—	94	540,000	30,000+	106	800,000	290,000+	157

43	37°	10,000	.....	100	6,000	4,000—	60	340,000	330,000+	3,400
	30°	20,000	10,000+	200	40,000	30,000+	400	310,000	300,000+	3,100
	20°	10,000	.....	100	10,000	.....	100	330,000	320,000+	3,300
44	37°	20,000	.....	100	30,000	10,000+	150	250,000	230,000+	1,250
	30°	30,000	10,000+	150	40,000	20,000+	200	370,000	350,000+	1,850
	20°	40,000	20,000+	200	60,000	40,000+	300	400,000	380,000+	2,000
45	37°	21,000	.....	100	12,000	9,000—	57	61,000	40,000+	290
	30°	55,000	34,000+	262	60,000	39,000+	276	61,000	40,000+	290
	20°	31,000	10,000+	148	50,000	29,000+	238	64,000	43,000+	305
46	37°	27,000	.....	100	34,000	7,000+	126	89,000	62,000+	330
	30°	101,000	74,000+	374	109,000	82,000+	404	130,000	103,000+	481
	20°	112,000	85,000+	415	121,000	94,000+	448	133,000	106,000+	493
47	37°	19,000	.....	100	32,000	13,000+	168	69,000	50,000+	363
	30°	25,000	6,000+	132	88,000	69,000+	463	52,000	33,000+	274
	20°	53,000	34,000+	279	76,000	57,000+	400	71,000	52,000+	373
48	37°	10,000	.....	100	9,000	1,000—	90	12,000	2,000+	120
	30°	10,000	.....	100	14,000	4,000+	140	11,000	1,000+	110
	20°	10,000	.....	100	10,000	.....	100	17,000	7,000+	170
49	37°	20,000	.....	100	24,000	4,000+	120	102,000	82,000+	510
	30°	20,000	.....	100	32,000	12,000+	160	31,000	11,000+	155
	20°	20,000	.....	100	17,000	3,000—	85	32,000	12,000+	160
50	37°	269,000	.....	100	84,000	185,000—	31	120,000	149,000—	45
	30°	307,000	38,000+	114	267,000	2,000—	99	229,000	40,000—	85
	20°	266,000	3,000—	99	300,000	31,000+	112	332,000	63,000+	123
51	37°	6,000	.....	100	4,000	2,000—	67	12,000	6,000+	200
	30°	17,000	11,000+	283	9,000	3,000+	150	13,000	7,000+	217
	20°	22,000	16,000+	366	12,000	6,000+	200	28,000	22,000+	467

Table 1 (*continued*)

Sample	Temperature (C.)	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
52	37°	75,000	.....	100	64,000	11,000—	85	143,000	68,000+	191
	30°	153,000	78,000+	204	171,000	96,000+	228	175,000	100,000+	233
	20°	149,000	74,000+	199	170,000	95,000+	227	197,000	122,000+	263
53	37°	86,000	.....	100	93,000	7,000+	108	172,000	86,000+	200
	30°	133,000	47,000+	155	121,000	35,000+	141	120,000	34,000+	140
	20°	134,000	48,000+	156	106,000	20,000+	123	113,000	27,000+	131
54	37°	82,000	.....	100	345,000	263,000+	421	369,000	287,000+	450
	30°	69,000	13,000—	84	396,000	314,000+	483	368,000	286,000+	449
	20°	76,000	6,000—	93	137,000	55,000+	167	213,000	131,000+	260
55	37°	6,000	.....	100	1,000	5,000—	17	16,000	10,000+	267
	30°	26,000	20,000+	433	9,000	3,000+	150	18,000	12,000+	300
	20°	8,000	2,000+	133	7,000	1,000+	117	8,000	2,000+	133
56	37°	26,000	.....	100	71,000	45,000+	273	73,000	47,000+	280
	30°	691,000	665,000+	2,658	830,000	804,000+	3,192	671,000	645,000+	2,581
	20°	458,000	432,000+	1,762	677,000	651,000+	2,604	497,000	471,000+	1,912
57	37°	102,000	.....	100	43,000	59,000—	42	69,000	33,000—	68
	30°	816,000	714,000+	800	967,000	865,000+	948	697,000	595,000+	683
	20°	1,159,000	1,057,000+	1,136	1,365,000	1,263,000+	1,338	1,653,000	1,551,000+	1,620
58	37°	110,000	.....	100	252,000	142,000+	229	146,000	36,000+	133
	30°	163,000	53,000+	148	341,000	231,000+	310	174,000	64,000+	158
	20°	194,000	84,000+	176	178,000	68,000+	162	110,000	.....	100
59	37°	56,000	.....	100	170,000	114,000+	304	357,000	301,000+	637
	30°	79,000	23,000+	141	240,000	184,000+	429	235,000	179,000+	420
	20°	109,000	53,000+	195	156,000	100,000+	279	92,000	36,000+	164

60	37°	13,000	.....	100	9,000	4,000—	70	51,000	38,000+	392
	30°	26,000	13,000+	200	19,000	6,000+	146	71,000	58,000+	546
	20°	20,000	7,000+	154	20,000	7,000+	154	37,000	24,000+	285
61	37°	8,000	.....	100	7,000	1,000—	87	168,000	160,000+	2,100
	30°	18,000	10,000+	225	11,000	3,000+	137	106,000	98,000+	1,325
	20°	12,000	4,000+	150	11,000	3,000+	137	58,000	50,000+	725
62	37°	6,000	.....	100	6,000	.....	100	6,000	.....	100
	30°	12,000	6,000+	200	8,000	2,000+	133	8,000	2,000+	133
	20°	7,000	1,000+	116	6,000	.....	100	9,000	3,000+	150
63	37°	28,000	.....	100	15,000	13,000—	54	28,000	.....	100
	30°	31,000	3,000+	111	25,000	3,000—	89	41,000	13,000+	146
	20°	20,000	8,000—	71	31,000	7,000—	75	22,000	6,000—	79
64	37°	45,000	.....	100	39,000	6,000—	87	50,000	5,000+	111
	30°	42,000	3,000—	93	63,000	18,000+	140	70,000	25,000+	155
	20°	30,000	15,000—	67	48,000	3,000+	107	36,000	9,000—	80
65	37°	22,000	.....	100	12,000	10,000—	55	21,000	1,000—	95
	30°	33,000	11,000+	150	30,000	8,000+	136	17,000	5,000—	77
	20°	23,000	1,000+	105	18,000	4,000—	82	36,000	14,000+	164
66	37°	490,000	.....	100	371,000	119,000—	76	795,000	305,000+	162
	30°	1,405,000	915,000+	286	525,000	35,000+	107	459,000	31,000—	94
	20°	767	489,233—	0.1	1,123	488,877—	0.2	1,308	488,692—	0.2
67	37°	76,000	.....	100	95,000	19,000+	126	83,000	7,000+	109
	30°	69,000	7,000—	91	87,000	11,000+	114	96,000	20,000+	126
	20°	86,000	10,000+	113	60,000	16,000—	79	50,000	26,000—	66
68	37°	6,000	.....	100	3,000	3,000—	50	3,000	3,000—	50
	30°	290,000	284,000+	4,833	100,000	94,000+	1,666	180,000	174,000+	3,000
	20°	330,000	324,000+	5,500	360,000	354,000+	6,000	470,000	464,000+	7,833

TABLE 1 (*continued*)

Sample	Temperature (C.)	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
69	37°	51,000	.....	100	56,000	5,000+	110	58,000	7,000+	114
	30°	123,000	72,000+	241	99,000	48,000+	194	105,000	54,000+	206
	20°	99,000	48,000+	194	63,000	12,000+	124	66,000	15,000+	129
70	37°	25,000	.....	100	30,000	5,000+	120	30,000	5,000+	120
	30°	174,000	149,000+	696	146,000	121,000+	584	124,000	99,000+	496
	20°	177,000	152,000+	708	125,000	100,000+	500	131,000	106,000+	524
71	37°	87,000	.....	100	120,000	33,000+	138	157,000	70,000+	180
	30°	380,000	293,000+	437	338,000	251,000+	389	322,000	235,000+	370
	20°	407,000	320 000+	469	350,000	263,000+	402	358,000	271,000+	411
72	37°	7,000	.....	100	3,000	4,000—	43	2,000	5,000—	29
	30°	13,000	6,000+	186	15,000	8,000+	214	7,000	.....	100
	20°	2,000	5,000—	29	5,000	2,000—	71	5,000	2,000—	71
73	37°	8,000	.....	100	6,000	2,000—	75	6,000	2,000—	75
	30°	12,000	4,000+	150	10,000	2,000+	125	8,000	.....	100
	20°	8,000	.....	100	8,000	.....	100	7,000	1,000—	87
74	37°	14,000	.....	100	12,000	2,000—	86	8,000	6,000—	57
	30°	28,000	14,000+	200	27,000	13,000+	193	17,000	3,000+	121
	20°	21,000	7,000+	150	14,000	.....	100	20,000	6,000+	142
75	37°	3,000	.....	100	1,000	2,000—	33	4,000	1,000+	133
	30°	6,000	3,000+	200	5,000	2,000+	167	3,000	.....	100
	20°	3,000	.....	100	2,000	1,000—	67	1,000	2,000—	33
76	37°	28,000	.....	100	23,000	5,000—	82	25,000	3,000—	89
	30°	91,000	63,000+	325	66,000	38,000+	235	64,000	36,000+	229
	20°	64,000	36,000+	229	66,000	38,000+	235	65,000	37,000+	234

77.....	37°	6,000	.....	100	7,000	1,000+	117	19,000	13,000+	317
	30°	1,393,000	1,387,000+	23,217	983,000	977,000+	16,383	1,077,000	1,071,000+	17,950
	20°	830,000	824,000+	13,833	1,050,000	1,044,000+	17,500	967,000	961,000+	16,117
78.....	37°	2,000	.....	100	1,000	1,000—	50	1,000	1,000—	50
	30°	8,000	6,000+	400	6,000	4,000+	300	8,000	6,000+	400
	20°	5,000	3,000+	250	3,000	1,000+	150	3,000	1,000+	150
79.....	37°	20,000	.....	100	306,000	286,000+	1,530	309,000	289,000+	1,545
	30°	105,000	85,000+	525	449,000	429,000+	2,245	333,000	313,000+	1,665
	20°	184,000	164,000+	920	442,000	422,000+	2,210	163,000	143,000+	815
80.....	37°	110,000	.....	100	100,000	10,000—	91	84,000	26,000—	76
	30°	199,000	89,000+	181	169,000	59,000+	154	132,000	22,000+	120
	20°	171,000	61,000+	155	176,000	66,000+	160	151,000	41,000+	137
81.....	37°	19,000	.....	100	373,000	354,000+	1,963	348,000	329,000+	1,831
	30°	37,000	18,000+	195	379,000	360,000+	1,994	404,000	385,000+	2,126
	20°	22,000	3,000+	116	365,000	346,000+	1,921	336,000	317,000+	1,768
82.....	37°	190,000	.....	100	130,000	60,000—	68	720,000	530,000+	379
	30°	160,000	30,000—	84	210,000	20,000+	110	320,000	130,000+	168
	20°	200,000	10,000+	105	230,000	40,000+	121	240,000	50,000+	126
83.....	37°	412,000	.....	100	417,000	5,000+	101	372,000	40,000—	90
	30°	850,000	438,000+	206	715,000	303,000+	176	975,000	563,000+	237
	20°	962,000	550,000+	233	740,000	328,000+	180	884,000	472,000+	214
84.....	37°	15,000	.....	100	15,000	.....	100	21,000	6,000+	140
	30°	58,000	43,000+	387	44,000	29,000+	295	73,000	58,000+	486
	20°	52,000	37,000+	347	31,000	16,000+	207	42,500	27,500+	283
85.....	37°	13,000	.....	100	10,000	3,000—	77	34,000	21,000+	261
	30°	23,000	10,000+	177	23,000	10,000+	177	29,000	16,000+	223
	20°	18,000	5,000+	138	14,000	1,000+	108	35,000	22,000+	269

TABLE 1 (*continued*)

Sample	Temperature (C.)	Plain agar	Difference	Approximate per cent	Lactose	Difference	Approximate per cent	Dextrose	Difference	Approximate per cent
86	37°	5,000	.....	100	6,000	1,000+	120	17,000	12,000+	340
	30°	8,000	3,000+	160	7,000	2,000+	140	16,000	11,000+	320
	20°	10,000	5,000+	200	7,000	2,000+	140	27,000	22,000+	540
87	37°	27,000	.....	100	15,000	12,000—	56	34,000	7,000+	126
	30°	191,000	164,000+	707	171,000	144,000+	633	138,000	111,000+	511
	20°	229,000	202,000+	848	161,000	134,000+	596	129,000	102,000+	478
88	37°	41,000	.....	100	32,000	9,000—	78	59,000	18,000+	144
	30°	319,000	278,000+	778	340,000	299,000+	829	498,000	457,000+	1,215
	20°	512,000	471,000+	1,249	774,000	733,000+	1,888	751,000	710,000+	1,832
89	37°	6,000	.....	100	9,000	3,000+	150	10,000	4,000+	167
	30°	59,000	53,000+	383	40,000	34,000+	667	87,000	81,000+	1,450
	20°	56,000	50,000+	933	44,000	38,000+	733	44,000	38,000+	733
90	37°	401,000	.....	100	468,000	67,000+	117	467,000	66,000+	116
	30°	6,000	395,000—	1	6,000	395,000—	1	19,000	382,000—	5
	20°	8,000	393,000—	2	10,000	391,000—	2	17,000	384,000—	4
91	37°	609,000	.....	100	751,000	142,000+	123	572,000	37,000—	94
	30°	2,497,000	1,888,000+	410	1,544,000	935,000+	253	937,000	328,000+	154
	20°	4,019,000	3,410,000+	660	5,660,000	5,051,000+	929	4,238,000	3,629,000+	696
92	37°	331,000	.....	100	382,000	51,000+	115	398,000	67,000+	120
	30°	434,000	103,000+	131	499,000	78,000+	124	424,000	93,000+	128
	20°	420,000	89,000+	127	357,000	26,000+	108	477,000	146,000+	144
93	37°	328,000	.....	100	282,000	46,000—	86	247,000	81,000—	75
	30°	344,000	16,000+	105	257,000	71,000—	78	378,000	50,000+	115
	20°	330,000	2,000+	101	336,000	8,000+	102	351,000	23,000+	107

94.....	37°	27,000	.....	100	23,000	4,000—	85	39,000	12,000+	144
	30°	56,000	29,000+	207	55,000	28,000+	204	83,000	56,000+	307
	20°	60,000	33,000+	222	63,000	36,000+	233	106,000	79,000+	393
95.....	37°	374,000	.....	100	325,000	49,000—	87	319,000	55,000—	86
	30°	522,000	148,000+	140	518,000	144,000+	138	504,000	130,000+	135
	20°	511,000	137,000+	137	561,000	187,000+	150	425,000	51,000+	114
96.....	37°	30,000	.....	100	30,000	.....	100	290,000	260,000+	967
	30°	30,000	.....	100	10,000	20,000—	33	100,000	70,000+	333
	20°	3,000	27,000—	10	3,000	27,000—	10	3,000	27,000—	10
97.....	37°	40,000	.....	100	130,000	90,000+	325	30,000	10,000—	75
	30°	20,000	20,000—	50	6,000	34,000—	15	100,000	60,000+	250
	20°	6,000	34,000—	15	3,000	37,000—	7	3,000	37,000—	7
98.....	37°	30,000	.....	100	200,000	170,000+	667	3,980,000	3,950,000+	13,267
	30°	40,000	10,000+	133	40,000	10,000+	133	790,000	760,000+	2,633
	20°	20,000	10,000—	67	20,000	10,000—	67	100,000	70,000+	333
99.....	37°	33,000	.....	100	55,000	22,000+	167	67,000	34,000+	203
	30°	33,000	.....	100	55,000	22,000+	167	102,000	69,000+	309
	20°	49,000	16,000+	148	59,000	26,000+	179	66,000	33,000+	200
100.....	37°	20,000	.....	100	10,000	10,000—	50	100,000	80,000+	500
	30°	30,000	10,000+	150	30,000	10,000+	150	190,000	170,000+	950
	20°	40,000	20,000+	200	40,000	20,000+	200	310,000	290,000+	1,550

TABLE 2. SUMMARY OF HIGHEST AND LOWEST COUNTS FOUND ON EACH COMBINATION OF INCUBATION TEMPERATURE AND MEDIUM

Medium, and incubation temperature (C.)	Counts expressed as per cent	Total number of highest counts	Number of counts up to 200 per cent	Number of counts up to 500 per cent	Number of counts up to 1000 per cent	Number of counts up to 5000 per cent	Number of counts up to 10,000 per cent	Total number of lowest counts*
Plain 37°.....	100.0	0	0	0	0	0	0	21
Lactose 37°...	175.3	2	1	0	0	0	0	31
Dextrose 37°..	444.9	10	6	4	2	1	1	10
Plain 30°.....	519.1	17	11	1	1	1	1	2
Lactose 30°...	453.5	11	9	2	2	0	0	2
Dextrose 30°..	778.6	22	17	11	4	2	0	1
Plain 20°.....	411.4	12	3	2	0	0	0	4
Lactose 20°...	498.5	5	3	3	1	0	0	4
Dextrose 20°..	664.8	21	13	6	3	1	0	5
Total.....	.....	100	63	29	13	5	2	80

* Twenty samples in which more than one combination of temperature and medium gave the lowest results are not included in this summary.

The results given in table 1 may be compared in several ways to show the variation obtained from each medium and incubation temperature. The writers have preferred to make comparisons on the basis of the number of highest and lowest counts found under each condition and also to compare the average percentage variation in count of all samples, regarding the 37° count on plain agar as 100 per cent. These comparisons are given in table 2, in which the outstanding features are as follows: (1) from all samples, higher counts were obtained from some other medium and temperature combination than the 37° count on plain agar; (2) of these higher counts, 63 per cent were increased twofold, 29 per cent fivefold, 13 per cent tenfold, 5 per cent fiftyfold, and 2 per cent more than a hundredfold.

Comparing the effects of incubation temperatures on all media, it was found that 50 per cent of the highest counts were obtained at 30°, 38 per cent at 20°, and 12 per cent at 37°. Of the lowest counts recorded, 6.2 per cent were obtained at 30°, 16.2 per cent at 20°, and 77.6 per cent at 37°.

The results of the various compositions of media compared at all temperatures showed that 29 per cent of the highest counts were obtained on plain agar, 18 per cent on lactose agar, and 53 per cent on dextrose agar. Of the lowest counts recorded, 33.7 per cent were obtained on plain agar, 46.2 per cent on lactose agar, and 20.1 per cent on dextrose agar.

On the basis of the 37° plain-agar count, the counts for all samples, as represented by the average percentage figures, show variations ranging from less than a twofold increase, for lactose agar at 37°, to more than a sevenfold increase, for dextrose agar at 30°.

From these data it appears that dextrose agar at 30° or 20° has distinct advantages over any of the other combinations used, for obtaining higher counts. There is comparatively little choice between plain agar at 20° and 30°, and lactose agar at the same temperatures, altho plain agar at 30° seems to have a slight advantage in the number of highest counts and the average percentage increase. The 37° counts on all of the media are decidedly unfavorable in comparison with those of the other incubation temperatures. Dextrose agar, however, has evident advantages over plain and lactose agar at this temperature. The slight difference which is found between the two latter media at 37° is in favor of the lactose agar.

Variation in counts at 37° *C.*

While lower bacteria counts were found at 37° than at the lower incubation temperatures, it is recognized that longer incubation periods are necessary in order to develop higher counts at the lower temperatures. At the end of forty-eight hours, the 37° counts have frequently proved higher than those resulting from similar incubation periods at the lower temperatures. An additional incubation period of two or three days, however, has always been necessary in order to develop the higher counts at these lower temperatures. On the other hand, there is usually very little increase in the 37° count after the first forty-eight-hour period. These facts might easily be interpreted to mean that forty-eight hours at 37° represents a time-temperature relationship which cannot be reduced if the greatest growth in the shortest period of time is desired. This particular temperature and incubation period may therefore be looked upon as the minimum and cannot be changed without materially affecting the usefulness of the results. The exacting demands for inspection work, which have determined the use of the 37° forty-eight-hour count, are not

operative in research work, in which the longer incubation periods and lower temperatures are generally used. These longer incubation periods at lower temperatures are used for the purpose of obtaining maximum counts where immediate results are not essential. Since this is the main object, greater variations in time or temperature may be used without affecting the results to the same degree that they would be affected by similar variations in the 37° forty-eight-hour counts.

Recognizing the importance of maintaining the correct temperature for the 37° count, an attempt was made to find out what variations in counts would result from possible differences of temperature due to piling the individual plates in a compact mass, as compared with the results obtained by so arranging the plates as to allow free circulation of air around each one. The former condition occasionally exists in any laboratory, particularly when a large number of plates must be incubated at the same time. In these experiments, the capacity of the incubator was only about half utilized. The sources of heat in the incubator were at the bottom, two and one-half inches below the temporary floor, at the top, and on two sides. Variations in temperature to which individual plates might be exposed, therefore, would be due to the slow diffusion of the heat resulting from the diminished ventilation around the piles of plates.

For these comparisons, two samples of market milk containing approximately the same number of bacteria, and with no apparent differences in flora, were selected. A sufficient volume of a single dilution was made so that about 200 plates could be prepared from the same bottle. The samples were diluted with the object of obtaining between 30 and 400 colonies to the plate. All plates were poured from the same batch of plain agar. They were placed in the incubator so that consecutive numbers would lie next to each other. The average of the counts from plates bearing two consecutive numbers was considered as the count for a single sample.

In testing the effect of the free circulation of air during incubation, 200 plates were arranged in layers on wire screens with about one-half inch air space between each layer. The bottom layer was one and one-half inches from the floor of the incubator. A uniform temperature of 37° at two inches from the top, and the usual ventilation of the incubator were maintained thruout the forty-eight-hour period. The counts obtained from these samples are shown in table 3.

TABLE 3. BACTERIA COUNTS OBTAINED FROM 100 SAMPLES OF THE SAME MILK WHEN AIR HAD CIRCULATED FREELY AROUND EACH PLATE DURING INCUBATION

Sample	Bacteria per cubic centimeter	Sample	Bacteria per cubic centimeter
1	240,000	51	225,000
2	235,000	52	240,000
3	250,000	53	255,000
4	250,000	54	185,000
5	285,000	55	240,000
6	315,000	56	365,000
7	270,000	57	245,000
8	200,000	58	265,000
9	260,000	59	245,000
10	280,000	60	150,000
11	235,000	61	230,000
12	260,000	62	215,000
13	200,000	63	305,000
14	170,000	64	245,000
15	225,000	65	175,000
16	190,000	66	275,000
17	345,000	67	195,000
18	215,000	68	275,000
19	260,000	69	275,000
20	155,000	70	275,000
21	205,000	71	245,000
22	200,000	72	145,000
23	270,000	73	275,000
24	160,000	74	115,000
25	210,000	75	205,000
26	185,000	76	240,000
27	225,000	77	170,000
28	300,000	78	340,000
29	285,000	79	215,000
30	275,000	80	225,000
31	295,000	81	210,000
32	195,000	82	255,000
33	290,000	83	275,000
34	195,000	84	270,000
35	215,000	85	255,000
36	305,000	86	270,000
37	245,000	87	195,000
38	300,000	88	125,000
39	210,000	89	270,000
40	270,000	90	225,000
41	280,000	91	200,000
42	295,000	92	200,000
43	155,000	93	220,000
44	250,000	94	315,000
45	205,000	95	210,000
46	280,000	96	230,000
47	180,000	97	200,000
48	205,000	98	250,000
49	205,000	99	270,000
50	155,000	100	350,000

In testing the effect of piled plates, the procedure was as follows: Piles of 12 plates each were arranged in a solid block, 6 piles long and 3 piles wide, and containing, in all, 216 plates. The same uniformity of temperature at two inches from the top, and the same ventilation, were maintained in the incubator as in the first experiment. Likewise, the average of the counts of two adjacent plates in each pile was taken as the count for a single sample. The two bottom plates in each pile are not included in the results, as it was desirable to consider only the counts from the plates kept at the same distance from the bottom of the incubator as were those in the first experiment; therefore the results are given for only five samples to the pile. In table 4, which is constructed to show the relative position of each pile in the block, appear the results obtained for each sample, that is, the average of each two adjacent plates.

TABLE 4. Bacteria Counts Obtained from Samples of the Same Milk When Plates Were Piled in a Solid Block during Incubation

Pile 1	Pile 2	Pile 3	Pile 4	Pile 5	Pile 6
424,000	402,000	366,000	338,000	404,000	456,000
419,000	346,000	336,000	403,000	358,000	366,000
419,000	395,000	303,000	339,000	402,000	397,000
368,000	367,000	272,000	345,000	360,000	364,000
328,000	308,000	210,000	191,000	152,000	302,000
Average 392,000	364,000	297,000	323,000	335,000	377,000
Pile 7	**Pile 8**	**Pile 9**	**Pile 10**	**Pile 11**	**Pile 12**
400,000	364,000	360,000	319,000	307,000	331,000
369,000	316,000	235,000	313,000	318,000	306,000
393,000	373,000	79,000	245,000	290,000	348,000
354,000	157,000	35,000	126,000	33,000	323,000
350,000	15,000	7,000	9,000	11,000	309,000
Average 373,000	245,000	143,000	202,000	192,000	323,000
Pile 13	**Pile 14**	**Pile 15**	**Pile 16**	**Pile 17**	**Pile 18**
409,000	344,000	403,000	361,000	357,000	344,000
350,000	356,000	364,000	397,000	401,000	341,000
375,000	240,000	371,000	342,000	302,000	408,000
380,000	371,000	295,000	283,000	201,000	315,000
306,000	386,000	237,000	211,000	309,000	286,000
Average 364,000	339,000	334,000	319,000	294,000	339,000

The results given in tables 3 and 4 show some striking facts concerning the effect upon the counts of these two different methods of exposure of the plates to the uniform conditions of temperature and ventilation maintained in the incubator. In table 4 there is a marked difference in the results from all top samples and samples in the corner piles, as compared with those from the bottom of the piles and particularly from those at the bottom of the piles on the inside of the block. In order to show these variations in counts, the standard deviation, the coefficient of variability, and the probable error were calculated for the entire number of samples in each set and for certain groups of samples which were packed in the solid block. These mathematical expressions are shown in table 5.

TABLE 5. VARIATIONS IN COUNTS DUE TO METHODS OF PILING PLATES AS SHOWN BY COEFFICIENT OF VARIABILITY, STANDARD DEVIATION, AND PROBABLE ERROR

Samples used for calculations	Number of samples	Average count	Standard deviation	Probable error	Coefficient of variability (per cent)
Air space between all plates (table 3)	100	237,350*	±49,014*	33,059*	20.6
Plates in solid block, all samples (table 4)	90	307,000	±105,000	70,822	34.2
Samples in corner piles only (Nos. 1, 6, 13, 18)	20	368,000	±45,485	30,679	12.3
Samples in side piles only (Nos. 2, 3, 4, 5, 7, 12, 14, 15, 16, 17)	50	330,000	±64,000	43,168	19.4
Samples in center piles only (Nos. 8, 9, 10, 11)	20	195,000	±138,016	91,742	69.7
Samples from top plates of each pile	18	365,000	±39,200	26,440	10.7
Samples from bottom plates of each pile	18	201,000	±123,200	83,098	61.3

*Not comparable with corresponding figures from samples shown in the remainder of the table because of difference in bacterial content of the milk.

The significant figures in table 5 are those representing the coefficient of variability, altho the other figures contribute toward a more comprehensive understanding of the variations found in the different groups of samples. The coefficient of variability obtained from samples when a free circulation of air was allowed between the plates was 20.6 per cent; whereas this

variability was increased to 34.2 per cent from samples that were piled in a solid block. This variation of 34.2 per cent is the resultant of larger and smaller variations from compound groups of the entire block of plates. The coefficients of variability of 10.7 per cent and 12.3 per cent from samples on the tops of all piles and from all plates in the corner piles, respectively, when compared with the higher coefficients of variability of 19.4 per cent, 69.7 per cent, and 61.3, per cent from those samples in positions less favorably situated, certainly indicate an important consideration in judging the reliability of the 37° count.

In order to determine to what extent variations in temperature within the solid block of plates were responsible for discrepant counts, an attempt was made to obtain temperature records at different places in the pile with a recording thermometer. In the absence of a more delicate apparatus, temperatures were determined with a Tycos recording instrument. All necessary precautions were observed in order to duplicate the normal temperature conditions from which the foregoing counts were obtained. These records, showing the temperature for each hour until the desired temperature of 37° was reached, are shown in table 6. Determination 1 is made from the empty incubator at a point midway between the top and the bottom; determination 2 was made under the same conditions except that the bulb of the thermometer was placed inside a petri plate; determination 3 was obtained with the bulb inside the fifth plate from the bottom of a single pile of 12 plates; determination 4 was the result of having the bulb inside the fifth plate from the bottom of a pile corresponding to pile 13 in the block of plates shown in table 4; determinations 5 and 6 were produced from plates in the same position in piles corresponding to numbers 15 and 8, respectively, of the same table. The vertical distance from the top of the incubator to the plate containing the thermometer bulb is the same as that to one of the plates included in determining the average count of the fourth ample from the top.

TABLE 6. TEMPERATURES RECORDED EACH HOUR AT DIFFERENT PLACES IN A BLOCK OF TIGHTLY PACKED PETRI PLATES

(In degrees centigrade)

Determination	Temperature at start	Temperatures recorded after								
		1 hour	2 hours	3 hours	4 hours	5 hours	6 hours	7 hours	8 hours	9 hours
1	20.0°	35.0°	37.0°	.....	.....	.....	.....	.....	.....	.....
2	20.5°	35.5°	37.0°	.....	.....	.....	.....	.....	.....	.....
3	20.5°	31.0°	34.4°	36.0°	37.0°	.....	.....	.....	.....	.....
4	21.5°	29.4°	33.8°	35.5°	36.6°	37.0°	.....	.....	.....	.....
5	21.0°	27.0°	31.6°	33.8°	35.0°	35.5°	35.5°	36.0°	36.6°	37.0°
6	21.0°	25.0°	28.0°	31.0°	32.7°	34.4°	35.5°	35.5°	36.0°	37.0°

The temperature records clearly indicate the relative length of time required by plates in different positions to reach the normal temperature. If records from inside the block of plates could have been obtained readily, it is quite probable that the length of time necessary to reach 37° would have proved even greater than that shown by determination 6. The rapidity of the heat diffusion apparently did not suffice to heat the entire block of plates soon enough to prevent marked irregularities in the counts made from the inner piles of the block. This fact emphasizes the greater likelihood of discrepant results from overcrowded incubators, or from other causes which in any way reduce the ventilation around the interior plates. In the positions represented by determinations 5 and 6, the temperatures were below normal for nine hours. This period, during which the plates in these positions were below normal, amounts to approximately 19 per cent of the entire incubation period. Plates on the outside of the pile, however, remained below normal temperature for a much shorter period, and consequently their counts were much higher and more nearly uniform than those obtained from plates that had not been maintained at the normal temperature for the entire period.

Discussion

The wide range of variations in the counts obtained by different incubation temperatures and media emphasizes the inadequacies of any single combination of temperature and media for determining the maximum

bacteria counts from miscellaneous samples of milk. Plain agar at 37° for forty-eight hours is unquestionably the least favorable combination for this purpose; the use of lactose agar at this temperature appears to have few, if any, advantages over plain agar; and altho dextrose agar at 37° has distinct advantages over those media, nevertheless the majority of the results obtained from it are lower than those produced at 20° or 30° for five days.

For developing the maximum counts, dextrose agar at 30° for five days seems to be superior to any of the other combinations considered in this paper. This medium at 20° for five days is also preferable to plain or lactose agar at either 30° or 20°. The same lack of a distinct superiority of one of these latter two media over the other exists at the lower temperatures, as well as at 37°.

Counts obtained at 37° after forty-eight hours are probably subject to greater discrepancies than those obtained at the lower temperatures for longer periods of time. It has been shown that the normal variations in temperature thruout a mass of tightly packed plates is sufficient to cause as high as a fiftyfold variation from the same sample of milk; whereas only a threefold variation was found when the plates were arranged to allow a free circulation of air around each one. To avoid gross discrepancies, it is necessary, on the basis of the previous results, to provide such ventilation in 37° incubators as will heat each individual plate in a block at an approximately equal rate.

Possible variations in bacteria counts resulting from the present plate method of enumeration should not be considered as a condition eliminating their usefulness. Bacteria counts, together with the discrepancies to which they are subject, should be considered only with full knowledge of their limitations and of the fact that they constitute but one item of the evidence necessary to grade milk into distinct classes according to its wholesomeness and keeping quality.

In order to harmonize these variations with existing numerical bacterial standards, it is essential that all factors tending to cause variations and discrepancies be reduced to a minimum. Furthermore, results obtained from such manipulations, even tho necessitating the statement of fixed numbers, should be interpreted in a manner which recognizes the lack of intrinsic value of these numbers for denoting such exact degrees of bacterial quality as the statement of fixed numerical expressions implies.

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ATTACHMENT OF THE ABDOMEN TO THE THORAX IN DIPTERA

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CONTENTS

PAGE

Methods and technique 256
Material 257
Terminology 261
Generalizations 262
Discussion of parts 264
The mesothorax 264
The tergum 264
The pleuron 265
The sternum 266
The metathorax 266
The tergum 266
The pleuron 267
The sternum 269
The legs 269
The abdomen 270
General description 270
The tergites 270
The sternites 272
The spiracles 274
Species of anthomyids 275
Summary 275
Bibliography 279
Character summary chart . . . . . *facing* 282

ATTACHMENT OF THE ABDOMEN TO THE THORAX IN DIPTERA

ATTACHMENT OF THE ABDOMEN TO THE THORAX IN DIPTERA[1]

BENJAMIN P. YOUNG

Many excellent studies have been made by various investigators on the morphology of the thoracic sclerites of different groups of insects. A number of these investigators have covered the entire class Insecta with the hope of determining the ground plan on which a typical thoracic segment is based. Such investigators have done much toward establishing a uniform terminology for this particular part of insect anatomy. Other workers have limited themselves to the consideration of a smaller group, as the order or the family. But in no place in the literature has the writer been able to find a record of extensive studies on the order Diptera. Snodgrass (1909, a and b) and Crampton (1909) have each figured two species; others have made even briefer references to the group. As for comprehensive work on the relation of the anterior abdominal sclerites to those of the metathorax, nothing has been found, isolated text figures being the only contributions along this line.

Through this study, which had as its primary aim the homologizing of the abdominal and thoracic sclerites in species of each available family of the Diptera, it was hoped that something might be added to the morphological literature of the group. Among the indices to phylogeny, wing venation has come to be regarded as one of the most valuable because it is the most evident; the morphology of the genitalia has not been used as much because of the difficulties attending such studies, but at present it is gaining favor because of the desirability of using all available means in throwing light on the above-mentioned problem. Vestiture has been made use of, especially by dipterologists, but mostly for generic and specific characters. If the external morphology of this particular part of the exoskeleton can contribute but its share toward the history of the descent of the group, the writer will feel that his efforts have not been in vain.

Furthermore, systematists of the order are not in accord as to the

[1] This investigation was suggested by, and carried on under the direction and supervision of, Dr. O. A. Johannsen. The writer is indebted to him not only for many suggestions growing out of his experience with the order Diptera as a whole, but also for his sincere interest shown throughout the progress of the work.

number of abdominal segments in different families. Some have counted only definitive segments and used such for key characters, while others have taken into consideration the true number as indicated by the spiracles. One of the reasons for figuring herein the pleurites of the meso- and the metathorax and the sclerites of the proximal abdominal segments of some of the commoner species of fifty-seven families of this order, is to aid in bringing about uniformity in interpretation.

Having studied but a few species of each family, the writer cannot say that the characters of the one figure hold throughout the family, but nevertheless a typical species should afford external facies more or less characteristic of the family.

METHODS AND TECHNIQUE

Practically all of this study was made from dried specimens which had been soaked for from three hours to seven days in a 10-per-cent solution of potassium hydroxide. Some forms were already clear enough for study but were allowed to remain in the clearer for a few hours in order to relax them sufficiently for study and handling. The specimens were then washed in distilled water to which a few drops of acetic acid had been added, and preserved in 70-per-cent alcohol.

It was soon found impossible to see sutures in some forms, especially the smaller species, without dissection, and it was only after each form had been halved by a median longitudinal cut with a scalpel that the work progressed with dispatch. This operation, which was done under 70-per-cent alcohol, was followed by the removal of the viscera of each half, but during the latter operation close attention was given also to the tracheal branches leading to the spiracles in order to learn the position and number of these in the abdomen. The left half was then available for external study, while the right was reserved for internal study of phragmas, apodemes, and apophyses as an aid to the more definite location of sclerites.

The binocular microscope was used both in making dissections and for the study of specimens in 70-per-cent alcohol. Drawings were made on coordinate paper with the aid of an ocular micrometer laid off in squares. To insure the object's remaining in the same place, a small piece of plasticine, used in modeling, was stuck to the bottom of a watch glass and the fly was held against the bottom of the glass by means of two bent pins

stuck into the plasticine just above each end of the insect. For drawings requiring two or three hours this proved to be a very satisfactory method, as the alcohol remains clear for that length of time.

In each drawing an attempt was made to show all chitinized areas clear and all membranes stippled. There are sclerites to be found, however, in which it is difficult to class the integument as either chitinous or membranous. Assuming the membranous state to be the more primitive, increasing amounts of chitin laid down in membrane were represented by a decreasing amount of stippling, that is, by placing the dots farther and farther apart. All outlines, as well as sutures (using the term in a general sense), were shown in full lines, while all endoskeletal parts, such as phragmas, and all sutures covered over by other parts, such as appendages, were shown in the dot-and-dash line. In most figures the amount of development of the phragma between the meso- and the metatergum also was represented in this manner. Indistinct sutures and boundaries of chitinized areas which shade off into membrane, or vice versa, were represented by dotted lines. Spiracular openings were shown either with a crosshatched interior or with a fringed border.

Pencil drawings were inked on the coordinate paper and plates were made directly from these. Drawings were either enlarged or reduced in order that all plates might have one dimension, the length, uniform. Prints were made on contrast paper and the sclerites were labeled on these reproductions.

MATERIAL

The material on which this paper is based was all drawn from the collections in the Department of Entomology at Cornell University. Dissections have been preserved in alcohol and retained for reference.

For the convenience of systematists the figures are arranged in the order of the families to which each species belongs, as listed in Aldrich's *Catalogue of North American Diptera.*

Of the fifty-nine families according to Aldrich, one or more species from fifty-five have been studied and figured. In addition *Sciara ochrolabis* and *Piophila casei*, which are included by Aldrich under the families Mycetophilidae and Sepsidae, respectively, are figured and placed in the families Sciaridae and Piophilidae. The following families are not represented: Acanthomeridae, Apioceridae, Phycodromidae, and Nycteri-

biidae. The list which follows gives the family, the species, the sex, and a reference to the drawings made of each. In addition, information gathered during the study as to the number of abdominal spiracles and their location in membrane or chitin is included.

Order *Diptera*

Division *Proboscidae*

Orthorrhapha — Nemocera

Tipulidae. *Pedicia albivitta*, female (Plate IX, 1 and 2), eight abdominal spiracles, all but last in membrane. It is possible that the supposed eighth spiracle may be the caudal attachment of the tracheal system to the tergite.

Pachyrrhina ferruginea, male (Plate IX, 3), seven abdominal spiracles, all in membrane.

Rhyphidae. *Trichocera brumalis*, female (Plate X, 4), seven abdominal spiracles, all in membrane.

Dixidae. *Dixa modesta*, female (Plate X, 5), seven abdominal spiracles, all in membrane.

Psychodidae. *Psychoda slossoni*, female (Plate X, 6), seven abdominal spiracles, all in membrane.

Chironomidae. *Chironomus ferrugineavitta*, male (Plate XI, 7 and 8), at least seven and possibly eight abdominal spiracles, all in membrane.

Culicidae. *Culex canadensis*, male (Plate XI, 9), seven abdominal spiracles, all in membrane.

Anopheles quadrimaculata, female (Plate XII, 10), seven abdominal spiracles, all in membrane.

Corethra albipes, female (Plate XII, 11), seven abdominal spiracles, all in membrane.

Mycetophilidae. *Leia winthemi*, female (Plate XII, 12), seven abdominal spiracles, all in membrane.

Sciaridae. *Sciara ochrolabis*, male (Plate XIII, 13), seven abdominal spiracles, all in membrane.

Cecidomyiidae. *Rhabdophaga strobiloides*, male (Plate XIII, 14), seven abdominal spiracles, all in membrane.

Bibionidae. *Plecia heteroptera*, female (Plate XIII, 15), eight abdominal spiracles, all in membrane.

Simuliidae. *Simulium hirtipes*, male (Plate XIV, 16), seven abdominal spiracles, all but first in membrane.

Blepharoceridae. *Blepharocera tenuipes*, female (Plate XIV, 17), seven abdominal spiracles, all in membrane.

Orphnephilidae. *Orphnephila americana*, female (Plate XIV, 18), seven abdominal spiracles, all in membrane. Semblance of eighth spiracle indicated by color but no spiracular opening to be seen.

Orthorrhapha — Brachycera

Stratiomyiidae. *Allognosta fuscitarsis*, female (Plate XV, 19), seven abdominal spiracles, all in membrane.

Tabanidae. *Chrysops indus*, male (Plate XV, 20), seven abdominal spiracles, all in membrane.

Leptidae. *Chrysopila ornata*, male (Plate XV, 21), seven abdominal spiracles, all in membrane.

Nemistrinidae. *Hirmoneura* sp., female (Plate XVI, 22), seven abdominal spiracles, all in membrane.

Cyrtidae. *Oncodes incultus*, female (Plate XVI, 23), six abdominal spiracles, all in chitin.

Bombylidae. *Anthrax alternata*, female (Plate XVI, 24), seven abdominal spiracles, all in membrane.

Therevidae. *Thereva fucata*, male (Plate XVII, 25), seven abdominal spiracles, all in membrane.

Scenopinidae. *Scenopinus fenestralis*, female (Plate XVII, 26), at least seven and possibly eight abdominal spiracles, probably all in membrane, although those of last four segments (considering eight spiracles) are very close to the chitinous margin of the sternites.

Midaidae. *Midas clavatus*, female (Plate XVII, 27), eight abdominal spiracles, all in membrane except last which is surrounded by chitin.

Asilidae. *Leptogaster loewi*, female (Plate XVIII, 28), at least seven and possibly an eighth abdominal spiracle, all except eighth in membrane.

Dolichopodidae. *Dolichopus cuprinus*, male (Plate XVIII, 29), seven abdominal spiracles, all in membrane.

Empididae. *Rhamphomyia* sp., female (Plate XVIII, 30), seven abdominal spiracles, all in membrane.

Lonchopteridae. *Lonchoptera* sp., female (Plate XIX, 31), seven abdominal spiracles, last four in membrane.

Phoridae. *Phora concinna*, female (Plate XIX, 32), at least six and possibly seven abdominal spiracles, all in membrane.

Cyclorrhapha — Athericera

Platypezidae. *Platypeza velutina*, female (Plate XIX, 33), seven abdominal spiracles, first, fifth, sixth, and seventh in membrane.

Pipunculidae. *Pipunculus atlanticus*, female (Plate XX, 34), seven abdominal spiracles, all in membrane.

Syrphidae. *Syrphus americanus*, male (Plate XX, 35), seven abdominal spiracles, all in membrane.

Conopidae. *Myopa vesiculosa*, male (Plate XX, 36), seven abdominal spiracles, all but sixth and seventh in membrane.

Cyclorrhapha — Calyptratae

Oestridae. *Gastrophilus intestinalis*, female (Plate XXI, 37), seven abdominal spiracles, all in membrane.

Tachinidae. *Tachina mella*, female (Plate XXI, 38), seven abdominal spiracles, sixth only in membrane although first is in very light chitin.

Dexiidae. *Thelaira nigripes*, male (Plate XXI, 39), seven abdominal spiracles, probably all in chitin although first, sixth, and seventh are in very light chitin.

Sarcophagidae. *Sarcophaga communis*, male (Plate XXII, 40), seven abdominal spiracles, first and sixth alone in membrane.

Muscidae. *Muscina stabulans*, female (Plate XXII, 41), seven abdominal spiracles, first, sixth, and seventh only in membrane.

Anthomyiidae. *Macrorchis ausoba*, male (Plate XXII, 42), seven abdominal spiracles, all in chitin.

Chortophila cilicrura, male (Plate XXIII, 43), seven abdominal spiracles, first and sixth in membrane.

Hylephila paludis, female (Plate XXIII, 44), seven abdominal spiracles, first, sixth, and seventh in membrane.

Schoenomyza dorsalis, female (Plate XXIII, 45), apparently only five abdominal spiracles, all in chitin. Small species, caudal spiracles may have been overlooked.

Ophyra leucostoma, male (Plate XXIII, 46), seven abdominal spiracles, first and sixth only in membrane.

Lispa sociabilis, female (Plate XXIII, 47), but five abdominal spiracles, first only in membrane.

Limnophora aequifrons, male (Plate XXIII, 48), seven abdominal spiracles, sixth only in membrane.

Eremomyia cylindrica, female (Plate XXIV, 49), seven abdominal spiracles, first only in membrane, although last two, which are rather close together, penetrate very light chitin.

Pegomyia affinis, female (Plate XXIV, 50), seven abdominal spiracles, first only in membrane, although last two, which are close together, penetrate very light chitin.

Hylemyia lipsia, female (Plate XXIV, 51), seven abdominal spiracles, first only in membrane, although sixth and seventh are located very close together in the weak chitin of the first telescoped segment of the ovipositor.

Anthomyia radicum, male (Plate XXIV, 52), seven abdominal spiracles, first and sixth in membrane.

Hebecnema umbratica, female (Plate XXIV, 53), but five abdominal spiracles found, first only in membrane.

Fannia canicularis, male and female, seven abdominal spiracles, first only in membrane.

Cyclorrhapha — Acalyptratae

Scatophagidae. *Scatophaga stercoraria*, male (Plate XXV, 54), seven abdominal spiracles, first and seventh in membrane.

Heteroneuridae. *Clusia lateralis*, female (Plate XXV, 55), seven abdominal spiracles, first five in membrane.

Helomyzidae. *Leria serrata*, male (Plate XXV, 56), seven abdominal spiracles, all in membrane.

Borboridae. *Borborus equinus*, female (Plate XXVI, 57), seven abdominal spiracles, all in membrane.

Sciomyzidae. *Dictya umbrarum*, female (Plate XXVI, 58), seven abdominal spiracles, all but last two in membrane.

Sapromyzidae. *Sapromyza lupulina*, male (Plate XXVI, 59), seven abdominal spiracles, all in membrane.

Ortalidae. *Rivellia viridulans*, female (Plate XXVII, 60), seven abdominal spiracles, all but last in membrane.

Rhopalomeridae. *Rhopalomera flaviceps*, female (Plate XXVII, 61), seven abdominal spiracles, all in membrane.

Trypetidae. *Euaresta festiva*, female (Plate XXVII, 62), seven abdominal spiracles, all but last in membrane.

Micropezidae. *Calobata albiceps*, female (Plate XXVIII, 63), seven abdominal spiracles, all but last in membrane.

Sepsidae. *Sepsis violacea*, female (Plate XXVIII, 64), seven abdominal spiracles, all but last two in membrane.

Piophilidae. *Piophila casei*, female (Plate XXVIII, 65), seven abdominal spiracles, all in membrane.

Psilidae. *Loxocera pleuritica*, male (Plate XXIX, 66), seven abdominal spiracles, all in membrane.

Diopsidae. *Sphyracephala brevicornis*, female (Plate XXIX, 67), seven abdominal spiracles, all in membrane.

Ephydridae. *Parydra limpidipennis*, female (Plate XXIX, 68), six abdominal spiracles, first only in membrane.

Oscinidae. *Chlorops* sp., male (Plate XXX, 69), six abdominal spiracles, first, second, and sixth only in membrane.

Drosophilidae. *Drosophila melanogaster* (*?*), female (Plate XXX, 70), seven abdominal spiracles, all in membrane.

Geomyzidae. *Anthomyza gracilis*, female (Plate XXX, 71), six abdominal spiracles found, all in membrane. Specimen so small that it was hard to be sure of no seventh spiracle.

Agromyzidae. *Agromyza lateralis*, male (Plate XXXI, 72), seven abdominal spiracles, all but last two in membrane. In female of species all but last one of seven spiracles are in membrane.

Division *Eproboscidae*

Hippoboscidae. *Melophagus ovinus*, female (Plate XXXI, 73), seven abdominal spiracles, all in membrane.

Olfersia americana, female (Plates XXXI, 74, and XXXII, 75), seven abdominal spiracles, all in membrane.

Order *Mecoptera*

Panorpidae. *Panorpa venosa*, female (Plate XXXII, 76), eight abdominal spiracles, all in membrane.

TERMINOLOGY

The rule of priority in the selection of anatomical terms is recognized in this paper only to the extent that these are descriptive of the parts to which they refer, or else have been so generally accepted by workers

in the group that the use of another more descriptive term would add to the confusion already existing in the nomenclatures of different orders of insects.

Full lines representing sutures in drawings are not limited to any one kind of suture, but to sutures in general, whether these are spaces between approximated sclerites or plates of the integument, impressed lines, or lines formed by the approximated lips of an infolding of the body wall.

GENERALIZATIONS

The scope of this investigation makes it necessary to limit the discussion of homologies to the metathorax and the first few abdominal segments; consequently many interesting modifications and details of structure in the remaining thoracic segments which have been figured may prove of advantage to those interested in the order, but must be disregarded at present by the writer. However, sclerites have been named in the mesothorax according to the dictates of this study, and a short discussion of the terms employed will of necessity be given.

If the Apterygote are to be considered the most generalized insects (forms in which wings were never present and therefore forms in which the muscular tension and mechanical stimulus due to the proper functioning of these locomotor appendages has never been experienced), and a thoracic segment of such an insect in which there is practically no chitin laid down in the membrane is to be considered as rather primitive, then our conclusion must be that a membranous condition must have been that of the thoracic segments of primitive insects, and only when the development of appendages gave rise to muscular stresses and strains and friction of parts was it necessary that their walls should be strengthened by the deposition of chitin in their integument. All theories to the origin of insects from annelid-like ancestors tend to strengthen this hypothesis. *Panorpa venosa* (Plate XXXII, 76), therefore, has been figured simply to show the appearance of a more primitive winged form. The development of wings has meant the chitinization of terga and pleura, together with the invagination of the body wall to form the pleural ridges, while the increase in size of the legs has meant their chitinization and their division into the true coxae and mera. The straightness of the pleural and coxal ridges is a mark of primitiveness. The large amount of membrane in the abdomen is another, while the distinctiveness of the basalares and the subalares might be considered a third. The two divisions of each tergum of the

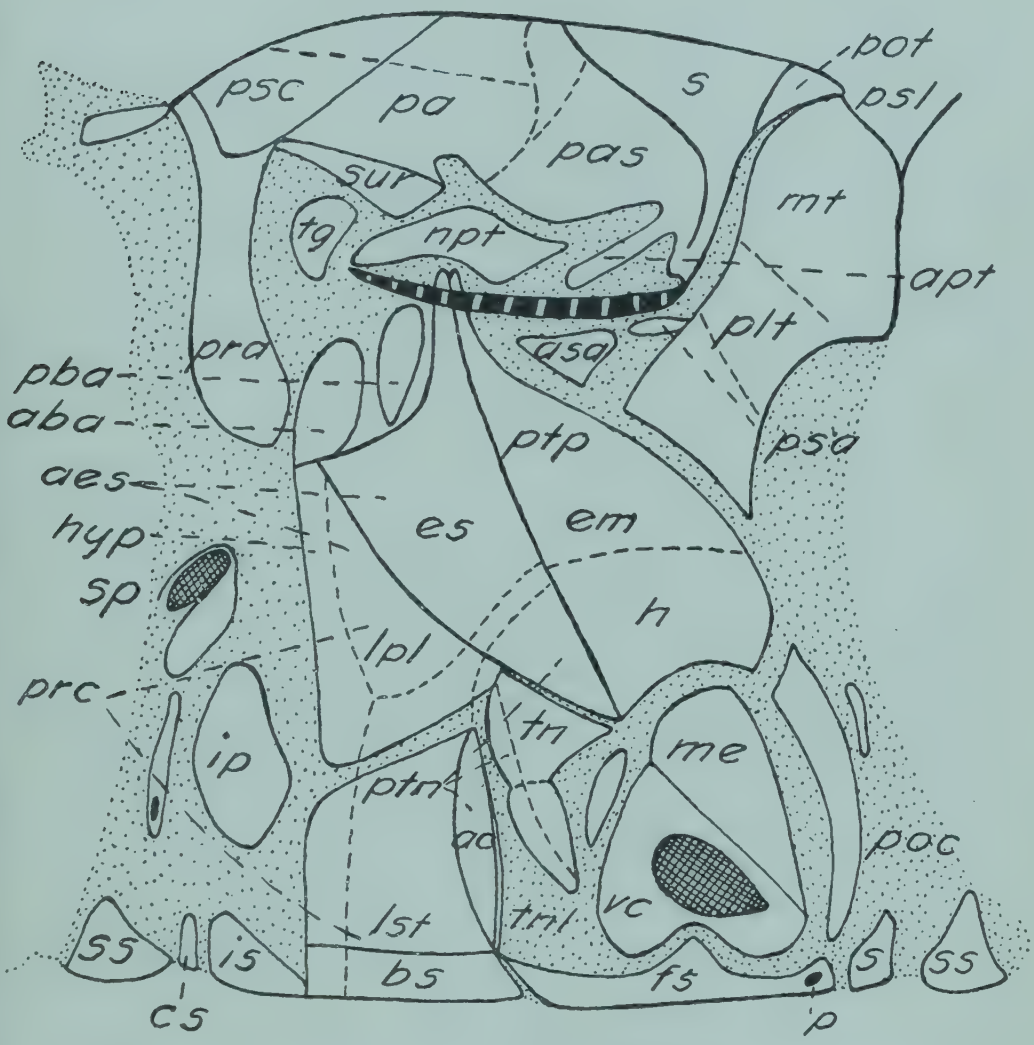

FIG. 21. GROUND PLAN OF A TYPICAL THORACIC SEGMENT IN WINGED INSECTS
(After Crampton, 1914_b)

meso- and the metathorax are clearly set off from each other, while the beginning in the development of phragmas is seen in both the anterior and the posterior infolding of the walls of the terga of these two thoracic segments. The maximum development of phragmas can be seen in the posterior mesothoracic and the anterior metathoracic one in some dipterous species.

For convenience in comparing, a copy of Crampton's (1914 b) "ground plan of a typical thoracic segment in winged insects" is here inserted (fig. 21). In the author's own words, this figure

represents an hypothetical composite type, to which the thoracic segments of any insect can be referred as a basis of comparison, rather than an attempted reconstruction of the original condition of the thoracic sclerites in the ancestors of winged insects. Most of the primitive features, however, are included in the figure, and to these have been added conditions found in the more specialized insects.

DISCUSSION OF PARTS

The mesothorax

The tergum

The two plates of the tergum as described by Verhoeff (1902) and by Snodgrass (1909 a) are readily distinguished in all forms figured. The large anterior plate, extending backward and including the axillary cord of Snodgrass (1909 b) and the post-tergite of Crampton (1914 b), composed largely of the scutum and the scutellum, has been called the scuto-scutellum when there are no visible divisions. Audouin (1824) has been followed herein in his divisions of the scuto-scutellum. The most anterior median region is termed the prescutum. The large central region, which is very often fused with the prescutum and also often subdivided by secondary sutures, is called the scutum. Laterally this division carries both the anterior and the posterior notal wing processes of Snodgrass, both of which are usually well defined in Diptera. The third division, known as the scutellum, is fairly constant as a narrow elevated median plate extending laterally into a narrow band bearing the axillary cord, which is continuous with the anal margin of the wing.

The small caudal division of the tergum when not divided is termed the postscutellum. This plate is often divided by sutures into a median and one or two lateral sclerites. When such is the case, only the abbreviations for these divisions appear on the drawings. For the middle plate the term *meditergite* (mt), and for the lateral plate or plates the term *pleuro-*

tergite (plt), are used. These are the terms which Crampton appropriates from Martin. In case there are two lateral plates formed, the writer has prefixed *ana* and *kata* to the term *pleurotergite* for the upper and lower subdivisions, respectively, calling the upper one *anapleurotergite* (aplt) and the lower one *katapleurotergite* (kplt).

The anterior phragma (Plate XXXII, 76, phg^2_a), or internal fold of the terga between the pro- and the mesothorax, is usually poorly developed in this group, and for this reason it is not indicated in the drawings. When present it usually projects under the pronotum. The posterior phragma (Plate XXXII, 76, phg^2_p) is well developed in the Brachycera (Plates XV, 21, and XVI, 24). Very frequently the two lamellae, the one of the mesonotum and the other of the metanotum, are easily distinguishable in the composition of this phragma.

The pleuron

Primarily the pleuron plate is composed of two sclerites, the episternum (es^2) and the epimeron (em^2). The suture (pleural) formed by a more or less transverse infolding of the walls of this plate (Plates IX, 1, and XI, 8, ap^2) divides it into an anterior part, the episternum, and a posterior region, the epimeron. This suture in its primitive condition extends from the wing process to the coxa, but in some of the higher Diptera, as *Muscina stabulans* (Plate XXII, 41), it may disappear altogether just above the leg. The primitive straightness of this suture as shown in *Panorpa venosa* (Plate XXXII, 76), in the Tipulidae (Plate IX, 3), in the Rhyphidae (Plate X, 4), in the Culicidae (Plate XII, 10), and in other forms, gives way in the more specialized members of the group to a prominent forward bending, in some cases, about midway dorsad from its origin at the coxa (Plates XX, 35, and XXII, 42).

Secondary sutures may divide either the episternum or the epimeron, or both, into a dorsal and a ventral region, and in some cases the dorsal episternal area into an anterior and a posterior part. If common usage did not dictate differently, the writer would prefer to use the more descriptive prefixes *ana* and *kata* combined with the names of the primary sclerites in referring to these secondary divisions, and simply refer to the secondary division of the dorsal episternum as the *anterior anepisternum*. But because of their widespread acceptance by systematists of this group, the use of Osten-Sacken's (1884) terms *pteropleura* and *sternopleura* —

slightly modified to *pteropleurite* (ptp^2) and *sternopleurite* (stp^2) as suggested by Crampton (1914 b) for *anepimeron* and *katepisternum*, respectively — seems advisable. Furthermore, Crampton's term *hypoepimeron* (hem^2) has been accepted on the same grounds. This leaves only the anepisternum to retain the more descriptive name, its anterior part being labeled "aes_a^2" and its posterior part when present being referred to as "aes_p^2".

The generalized type of coxa as illustrated in *Panorpa venosa* (Plate XXXII, 76) — in which the pleural suture is continuous throughout the length of this first segment of the leg, dividing it into the true coxa (cx^2) and the meron (me^2), terms used by Walton (1900) — is to be recognized only in a few of the lowest families of flies, as the Tipulidae (Plate IX, 2 and 3) and the Rhyphidae (Plate X, 4). In the last two figures evidence is given of the migration of the meron dorsad to become fused eventually with the lower pleural sclerite, the hypoepimeron. In all the higher families of flies this interpretation is placed on the fate of the meron, and the combined meron and hypoepimeron is termed, after Crampton (1914 b), the *meropleurite* (mep^2).

The basalare and subalare sclerites are often present in this order and are figured herein, although not labeled in most of the drawings.

The sternum

To the writer's mind it seems doubtful whether the term *sternopleurite* should be used as its author intended, that is, to refer to a combined sternal and pleural sclerite, or rather to the part of the pleurite which borders on the sternum. The study of the venter of flies is carried on with difficulty because of the proximity of the bases of the legs. But a number of the broader representatives of the group show the same arrangement of sclerites as does *Olfersia americana* (Plate XXXII, 75), in which the two pleurites termed *sternopleurites* meet each other on the ventral side, apparently crowding out the anterior part of the sternum — the *basisternite* (bs) of Crampton (1909). The furcasternite (fs) alone seems to remain in this group.

The metathorax

The tergum

Compared with those of the mesothorax, all three plates of the metathorax are very small. As has been suggested, the large development of

the mesothorax to take care of the powerful wing muscles seems to have taken place at the expense of the following thoracic segment. Especially is this evident in the tergal region, which usually consists of a narrow band of integument connecting the two halteres and providing a single lamella cephalad as its share in the formation of the mesothoracic postscutellar phragma (phg^2_p). It is impossible to make out the four principal subdivisions of the tergum in the metathorax of Diptera. This plate reaches its greatest development in *Psychoda slossoni* (Plate X, 6), so far as the writer's studies have gone. It may be continuous with the epimeron of this segment, as in *Plecia heteroptera* (Plate XIII, 15), *Scenopinus fenestralis* (Plate XVII, 26), *Leptogaster loewi* (Plate XVIII, 28), and many other species, or there may be a suture separating these two sclerites, as in *Anthrax alternata* (Plate XVI, 24), *Platypeza velutina* (Plate XIX, 33), *Macrorchis ausoba* (Plate XXII, 42), and many others; but practically in every case the tergum is separated from the episternum in this segment by the pleural suture.

The pleuron

Although comparatively small sclerites, the episternum (es^3) and the epimeron (em^3) are separated in the metathorax, as in the mesothorax, by the pleural suture. This infolding of the body wall is fairly constant in its extent from the coxae to the base of the halteres, and, studied from the inside, affords one of the best landmarks for homologizing these sclerites. Occasionally in the more generalized species the presence of secondary sutures in the episternal sclerite makes necessary the use of the terms *anepisternum* (aes^3) and *katepisternum* (kes^3), as in *Pachyrrhina ferruginea* (Plate IX, 3) and *Leia winthemi* (Plate XII, 12). Secondary sutures are present also in the posterior pleural sclerite, as in *Dixa modesta* (Plate X, 5) and *Culex canadensis* (Plate XI, 9), but because of the uncertainty as to the line of demarcation between the postscutellum and the epimeron the single term *epimeron* (em^3) is used here.

A large number of peculiarities or variations in the shape of the pleural sclerites are to be found in the various families of this order. Chief among these might be mentioned the following. Commonest of all, perhaps, is a greatly developed episternum with a resulting small epimeron, often nothing more than a narrow strip of chitin and in some cases resulting in the lower part of the epimeron becoming membranous throughout.

Examples of such a development are found in Plates IX, 2, X, 4, 5, and 6, XI, 7, XII, 12, XIII, 13, 14, and 15, XIV, 18, XVII, 27, and XIX, 32. On the other hand, there are examples of the opposite development, the epimeron becoming greatly enlarged at the expense of the episternum, as in *Dolichopus cuprinus* (Plate XVIII, 29).

Another common peculiarity in the epimeral region is the failure of the hypodermal cells of the ventral part of this area to lay down chitin in the integument, with the resulting appearance of the epimeron's moving dorsad (Plates X, 6, XI, 7, XIII, 14, XIV, 16, 17, and 18, XIX, 32, XX, 34 and 35, XXVI, 57, XXVII, 62, XXIX, 67). Many examples of very weak chitin in this lower epimeral sclerite are to be seen. In fact, it is often difficult to say where the epimeron leaves off and the intersegmental abdominal membrane begins (Plates XIII, 13, XXI, 38 and 39, XXII, 41, XXX, 70 and 71, XXXI, 72).

An interesting variation in the lower Nemocera, and one that is very difficult of interpretation, is the movement cephalad of the episternum (es^3) into the mesothorax, with a resulting crowding of the compound sclerite mep^2 into a very small area above the mesothoracic coxa (Plates X, 5 and 6, XI, 9, XII, 10 and 11).

The movement forward of both pairs of legs has caused a decided prolongation of both the episternum (es^3) and the epimeron (em^3) in *Leptogaster loewi* (Plate XVIII, 28) and in *Gastrophilus intestinalis* (Plate XXI, 37); while the prolongation of the coxae in *Leia winthemi* (Plate XII, 12) apparently results in the movement of the episternum (es^3) and the epimeron (em^3) down on the base of the legs.

Sutures sometimes become vestigial, as in the case of *Oncodes incultus* (Plate XVI, 23) in which the pleural suture shows no implex nor scarcely any external evidence of having once existed just above the base of the coxa. The suture between the lower epimeron of the mesothorax and the metathoracic episternum is lacking in *Dixa modesta* (Plate X, 5) and in *Phora concinna* (Plate XIX, 32).

What seemed to be sense pits were found on a number of species, on either the tergum or the pleuron of the metathorax or the basic segments of the abdomen. In a number of cases these have been figured, as in *Thereva fucata* (Plate XVII, 25, em^3 and 2s), in *Leptogaster loewi* (Plate XVIII, 28, t^3), in *Chrysopila ornata* (Plate XV, 21, 2t), and in *Hirmoneura* sp. (Plate XVI, 22, 2t and 2s).

The course of the metathoracic apodeme (Plate XI, 8, ap^3), together with the locations of the metathoracic spiracles (sp^3) and the first abdominal spiracle (1sp), has been a great aid in deciding on these relationships.

Besides the episternum and the epimeron, there is a third pleural sclerite in the metathorax of Diptera which seems to correspond to Crampton's (1914 b) compound sclerite, the pleurotrochantin (fig. 21, ptn.) This compound sclerite is described as being composed of the antecoxale (ac) — which is a narrow marginal strip of the basisternite — the trochantinelle (tnl), the trochantin (tn), and the lower part of the episternum. This sclerite is present in a large number of the higher Diptera, and especially is well marked in the acalyptrate muscids, as *Leria serrata* (Plate XXV, 56, ptn^3), *Rivellia viridulans* (Plate XXVII, 60, ptn^3), and *Sphyracephala brevicornis* (Plate XXIX, 67, ptn^3).

The sternum

As in the mesothorax, the furcasternite — the sternal region which bears the internal diapophyses, or furcae (Plate IX, 1, $apys^3$) — seems to be the only sternite remaining in the order. A glance at the ventral view of *Olfersia americana* (Plate XXXII, 75) will show the marginal lips of the two sclerites termed *pleurotrochantin* (ptn^3) meeting in the mid-ventral line but separating caudad to form the furcasternite (fs^3).

The legs

In no case was the metathoracic coxa found divided by a suture into the true coxa and the meron. If muscular tension causes the ridges of the body wall to be drawn inward for the formation of phragmas, apodemes, and apophyses, this may give a partial explanation of the disappearance of a suture dividing the coxa into two subdivisions, as the metathoracic muscles are greatly reduced in size due to the replacement of the wings by the halteres.

Nothing further need be said concerning the metathoracic legs, except that the coxae show the greatest variation. *Leia winthemi* (Plate XII, 12, cx^3) and *Sciara ochrolabis* (Plate XIII, 13, cx^3) show a considerably elongated condition. In *Blepharocera tenuipes* (Plate XIV, 17, cx^3) the coxae assume a diagonal position between the thorax and the trochanter, while innumerable variations in shape exist. A number of the Acalyptratae show this part of the leg fairly well sculptured with secondary external sutures,

as in *Scatophaga stercoraria* (Plate XXV, 54, cx^3), *Dictya umbrarum* (Plate XXVI, 58, cx^3), and *Sapromyza lupulina* (Plate XXVI, 59, cx^3).

The abdomen

General description

In taking up the discussion of the morphology of the abdomen in its relation to the thorax, the tergites, the sternites, and the spiracles are considered separately. There is little to be said in regard to the pleura aside from the fact that they are commonly taken as the membranous areas between chitinized tergites and sternites. Needless to say, this region shows a considerable variation in width in species showing some deposition of chitin in the sternites and the tergites. A comparison of *Calobata albiceps* (Plate XXVIII, 63) with one of the calyptrate muscids, as *Thelaira nigripes* (Plate XXI, 39), will at once show a wide difference. In the latter example the pleura consist only of narrow inflexed areas between the greatly enlarged tergites and the small sternites which they have overgrown. In the case of species showing no deposition of chitin in the sternal region, as *Phora concinna* (Plate XIX, 32) and *Chlorops* sp. (Plate XXX, 69), and in species showing no deposition of chitin in either the tergal or the sternal region, as *Orphnephila americana* (Plate XIV, 18), *Melophagus ovinus* (Plate XXXI, 73), and *Olfersia americana* (Plate XXXI, 74), it is impossible to speak of a definitive pleuron.

In homologizing the sclerites in the abdomen of Diptera the position of the spiracles is of invaluable aid. In fact, it would be next to impossible to be sure of the sclerites of the first segment without the location of the first abdominal spiracle. An internal study is often necessary to establish the position of this opening to the tracheal system.

In this order, usually five more or less definite abdominal segments may be seen. Beyond the fifth the segments are variously modified to form the genitalia. For this reason it is very easy to overlook spiracles beyond the fifth, as these are often small and show a tendency toward cephalization. It is not unusual to find those of successive segments crowded close together in the same segment in this region.

The tergites

There are many interesting features in the structure of the abdominal tergites. In looking at the group as a whole, it is quite evident that there is a tendency for the first tergite, as well as for the first sternite,

to decrease in relative size. This one is usually nothing more than a narrow band as compared with those that follow. (Plates IX, 2 and 3, X, 4, XIV, 17, XVI, 22, XVII, 26, XVIII, 28 and 30, XX, 35.) Nor can all of this decrease be attributed to the failure of the hypodermal cells to deposit chitin in the membrane just cephalad of the first tergite. It seems very probable that the belief that one segment may gradually disappear owing to the great development of a contiguous segment, is sometimes warranted.

This theory of growth of one segment at the expense of an adjoining one might at first seem to be very good evidence for use in determining what has happened in case of species which show but one chitinized tergite to two spiracles, such as *Lonchoptera* sp. (Plate XIX, 31, 1t and 2t), *Macrorchis ausoba* (Plate XXII, 42, 1t and 2t), *Euaresta festiva* (Plate XXVII, 62, 1t and 2t), *Calobata albiceps* (Plate XXVIII, 63, 1t and 2t), *Sepsis violacea* (Plate XXVIII, 64, 1t and 2t), *Piophila casei* (Plate XXVIII, 65, 1t and 2t), and *Sphyracephala brevicornis* (Plate XXIX, 67, 1t and 2t). But on considering the large number of examples that might be regarded as transitional stages between the well-defined first and second tergite, on the one hand, and the single tergite to represent both, on the other hand, it is easier to believe in a fused condition of these two tergites than in the alternative which would permit the second, or larger, tergite to crowd out the first, or smaller, one altogether. These transitory stages may be seen in a number of species. In *Platypeza velutina* (Plate XIX, 33) there appear two notches in the latero-ventral margin of the tergites at about the place where one would expect to find a dividing suture, and only a lighter band can be seen extending up through the middle of the tergites. In *Pipunculus atlanticus* (Plate XX, 34) the only remaining sign of a suture is a very faint impressed line. In *Tachina mella* (Plate XXI, 38), only a lighter-colored band marks what may have been the position of a suture in its progenitors. This is likewise the case in *Sarcophaga communis* (Plate XXII, 40). Very faint impressed lines exist in *Thelaira nigripes* (Plate XXI, 39), in *Muscina stabulans* (Plate XXII, 41), and in *Dictya umbrarum* (Plate XXVI, 58). Latero-ventral incisions, sometimes with and sometimes without vestigial sutures, are to be seen in some species, as *Sapromyza lupulina* (Plate XXVI, 59), *Parydra limpidipennis* (Plate XXIX, 68), *Chlorops* sp. (Plate XXX, 69), and *Drosophila melanogaster (?)* (Plate XXX, 70). A vestigial suture exists in *Rivellia viridulans* (Plate XXVII, 60), while only a bit of membrane is to be found in such

species as *Borborus equinus* (Plate XXVI, 57), *Rhopalomera flaviceps* (Plate XXVII, 61), and *Loxocera pleuritica* (Plate XXIX, 66). These and other examples that might be cited seem to warrant the consideration of this first definitive tergite as the fused first and second tergites. In unbleached specimens these indications of a suture would hardly be noticed, and so it is not to be wondered at that systematists of the order do not always agree as to the number of abdominal segments.

Another possible source of confusion to the systematist is to be found in the division of tergites into secondary parts, either by sutures or a strip of membrane. This may occur in either the first or the second segment. As an example of a tergite being divided into two subdivisions by a suture, one need only refer to the drawings of *Simulium hirtipes* (Plate XIV, 16, $1t_a$ and $1t_p$) and *Midas clavatus* (Plate XVII, 27, $1t_a$ and $1t_p$). Examples of division by membrane may be seen in *Sciara ochrolabis* (Plate XIII, 13, $1t_a$ and $1t_p$) and in *Plecia heteroptera* (Plate XIII, 15, $2t_a$ and $2t_p$). An example of the separation of the first and second tergites by a narrow band of membrane or weak chitin is given in *Allognosta fuscitarsis* (Plate XV, 19).

In several species the first abdominal tergite has so overgrown the thorax that on superficial examination it appears as a part of this region. This condition is most evident in such species as *Chrysops indus* (Plate XV, 20, 1t) and *Anthrax alternata* (Plate XVI, 24, 1t).

A very noticeable character, and one that was first found in *Myopa vesiculosa* (Plate XX, 36), is an adventitious suture arising from the latero-cephalic margin of the first abdominal tergite and running caudo-dorsad through this tergite often to the cephalic margin of the second tergite. This varies considerably in its degree of development in different species, but was found in all the species examined among both the Calyptratae and the Acalyptratae. Generally speaking, this suture is less highly developed in the calyptrate than in the acalyptrate muscids, as is seen on comparing *Thelaira nigripes* (Plate XXI, 39) and *Muscina stabulans* (Plate XXII, 41) with *Scatophaga stercoraria* (Plate XXV, 54) and *Sepsis violacea* (Plate XXVIII, 64).

The sternites

The greater demand made upon the tergites for the attachment of muscles than upon the sternites is clearly reflected in the larger number

of species found in which the sternites were composed of membrane or very weak chitin. In so far as the tergites are concerned, these are of such a composition only in *Orphnephila americana* (Plate XIV, 18); while the following species show this condition in so far as the sternites are concerned: *Simulium hirtipes* (Plate XIV, 16), *Orphnephila americana* (Plate XIV, 18), *Phora concinna* (Plate XIX, 32), *Gastrophilus intestinalis* (Plate XXI, 37), *Chlorops* sp. (Plate XXX, 69), *Melophagus ovinus* (Plate XXXI, 73), and *Olfersia americana* (Plate XXXI, 74). Instances of the first abdominal tergite remaining membranous, possibly to facilitate the movement of the caudal end of the abdomen, are not uncommon. This is the case in *Anopheles quadrimaculata* (Plate XII, 10), *Midas clavatus* (Plate XVII, 27), *Lonchoptera* sp. (Plate XIX, 31), *Pipunculus atlanticus* (Plate XX, 34), and *Borborus equinus* (Plate XXVI, 57). Other species, such as *Rhabdophaga strobiloides* (Plate XIII, 14) and *Drosophila melanogaster* (*?*) (Plate XXX, 70), have a slight amount of chitin laid down in this sternite.

The same forces that have had their effect in decreasing the size of the first abdominal tergites have produced the same result in the sternites of a larger number of species. Most decidedly is this the case in *Trichocera brumalis* (Plate X, 4, 1s), in *Thereva fucata* (Plate XVII, 25, 1s), in *Scenopinus fenestralis* (Plate XVII, 26, 1s), in *Leptogaster loewi* (Plate XVIII, 28, 1s), in *Dolichopus cuprinus* (Plate XVIII, 29, 1s), and in *Muscina stabulans* (Plate XXII, 41, 1s); while the same condition holds to a lesser extent in *Leia winthemi* (Plate XII, 12, 1s), in *Sciara ochrolabis* (Plate XIII, 13, 1s), in *Hirmoneura* sp. (Plate XVI, 22, 1s), and in *Sarcophaga communis* (Plate XXII, 40, 1s).

Subdivisions of primary sternites are found oftener than are subdivisions of primary tergites, the second sternite being the one oftenest modified in this way. In *Pachyrrhina ferruginea* (Plate IX, 3, $1s_a$ and $1s_p$), in *Plecia heteroptera* (Plate XIII, 15, $2s_a$ and $2s_p$), in *Rhamphomyia* sp. (Plate XVIII, 30, $2s_a$ and $2s_p$), and in *Calobata albiceps* (Plate XXVIII, 63, $2s_a$ and $2s_p$), the anterior part is separated from the posterior part of the second sternite by membrane.

In only one species, *Chrysops indus* (Plate XV, 20, 1s and 2s), were the first and second sternites found to have coalesced. Here a double row of sense pits marks the usual position of the suture between the first and the second segment.

The spiracles

The number of abdominal spiracles in Diptera varies from five to eight, with seven as the number oftenest met with. Data on this point are given in the list of species on pages 258 to 261. A glance at these data will show these openings to the tracheal system appearing either in membrane or in chitin, but oftener in membrane, as would be expected when it is considered that the normal position of the row of abdominal spiracles may be assumed to be midway between dorsum and venter in the latus. In a large majority of families this region remains membranous, and only in relatively few have the so-called tergites usurped the pleural region enough to include the spiracles. It amounts to this: when the hypodermal cells in the pleural region have become stimulated enough to deposit chitin, then, in the order Diptera, this region forfeits its right to be known as a part of the pleuron and must be called a part of the tergum. This arrangement of spiracles in the order certainly goes to show that if for any reason there is need for rigidity in a certain region, it is no more difficult to lay down chitin around spiracles than at any other place.

As a rule it may be said that the abdominal spiracles of species of the Nemocera and Brachycera groups in the suborder Orthorrhapha are to be found in membrane. But immediately the outstanding exceptions, in so far as the writer's study has gone, would have to be mentioned in *Oncodes incultus* (Plate XVI, 23) and in *Lonchoptera* sp. (Plate XIX, 31). In the suborder Cyclorrhapha, the representative families of the Athericera and the Acalyptratae tend to permit their abdominal spiracles to remain in membrane. A number of exceptions would have to be raised here, however, such as *Platypeza velutina* (Plate XIX, 33), *Parydra limpidipennis* (Plate XXIX, 68), and others. Among the families of the Calyptratae of this suborder, the tendency is toward the deposition of chitin about these spiracular openings because of the excessive downward extension of the tergites. It is needless to say that this is not the case in all species of every family in the group. A glance at the record of the species of anthomyids studied will expel any doubts concerning this last statement.

In most of the Diptera, and especially in the more generalized species, the first abdominal spiracle is to be found in the anterior part of the segment and very often in the membrane between the metathorax and the first abdominal segment. The usual position of the remaining spiracles is

near the middle of the segment, if anything slightly cephalad from the center. Such an arrangement as that in *Oncodes incultus* (Plate XVI, 23), in which the first abdominal spiracle appears in the posterior part of the segment, is very unusual, while examples of the shifting of all spiracles to the anterior end, as in *Allognosta fuscitarsis* (Plate XV, 19), is not at all uncommon.

SPECIES OF ANTHOMYIDS

Because of the uncertain systematic position of some genera within the family Anthomyiidae, species of twelve genera of this family were studied and figured (Plates XXII, 42, XXIII, and XXIV, inclusive). Considerable uniformity is shown in the structure of the region around the base of the abdomen. In each case were the episternum (es^3) and the epimeron (em^3), as well as the pleurotrochantin (ptn^3), of the metathorax clearly defined. The fused condition of the first and second abdominal tergites, in contrast to the separate state of the corresponding sternites, held in each. Also, the adventitious suture of the first abdominal tergite was constant. The greatest variation found in these species, perhaps, was in the location of the abdominal spiracles. This can be seen by referring to the information concerning abdominal spiracles which accompanies each species in the list on pages 258 to 261.

SUMMARY[2]

Points brought out in a summary of an investigation of this nature must of necessity be based upon a study of a rather limited amount of material, considering the number of genera and species in the entire order. However, uniformities existing in single species of so wide a range of families as the writer has been permitted to examine, will at least suggest points to be tested in a wider range of species within certain families. Furthermore, they cannot help adding their bit in the task of unraveling the phylogeny of the order Diptera.

One of the most interesting characteristics to appear in a large number of families is what has been termed an adventitious suture, or a suture running caudo-dorsad from the anterior margin of the first abdominal tergite and one not to be confused with the suture dividing the first and the second tergite although the two are closely related to each other.

[2]The chart from which this summary was deducted is inserted at the end of this paper.

This suture was found in species of all the families studied among the Calyptratae and the Acalyptratae, but in only one family outside of these two groups, in *Myopa vesiculosa* (Plate XX, 36) of the family Conopidae.

Closely associated with the appearance of this suture is a tendency toward the coalescence of the first two abdominal tergites. This tendency toward fusion occurs in all the families of the Acalyptratae with the exception of the Scatophagidae (Plate XXV, 54), the Heteroneuridae (Plate XXV, 55), and the Helomyzidae (Plate XXV, 56); and in all the families of the Calyptratae with the exception of the Oestridae (Plate XXI, 37). Aside from the families of these two groups it occurs only in the Conopidae (Plate XX, 36), the Pipunculidae (Plate XX, 34), the Platypezidae (Plate XIX, 33), and the Lonchopteridae (Plate XIX, 31). But at least five different stages in the development of this tendency can be pointed out if there are included the families showing both the adventitious suture and a complete suture between the first and second tergites, as the Oestridae (Plate XXI, 37), the Scatophagidae (Plate XXV, 54), the Heteroneuridae (Plate XXV, 55), and the Helomyzidae (Plate XXV, 56). The adventitious suture and only the dorsal part of the suture dividing the two tergites are found in the Conopidae (Plate XX, 36), the Sarcophagidae (Plate XXII, 40), the Sciomyzidae (Plate XXVI, 58), the Piophilidae (Plate XXVIII, 65), and the Geomyzidae (Plate XXX, 71). Further, the adventitious suture and only the ventral part of the suture dividing the first and second tergites are found in the Borboridae (Plate XXVI, 57), the Sapromyzidae (Plate XXVI, 59), the Ortalidae (Plate XXVII, 60), the Sepsidae (Plate XXVIII, 64), the Ephydridae (Plate XXIX, 68), the Oscinidae (Plate XXX, 69), and the Drosophilidae (Plate XXX, 70). The next stage would be represented by families showing the adventitious suture alone, in a few cases the suture between the tergites being represented by a semblance of membrane, as in the Tachinidae (Plate XXI, 38), the Dexiidae (Plate XXI, 39), the Muscidae (Plate XXII, 41), the Anthomyiidae (Plate XXII, 42), the Rhopalomeridae (Plate XXVII, 61), the Trypetidae (Plate XXVII, 62), the Micropezidae (Plate XXVIII, 63), the Psilidae (Plate XXIX, 66), the Diopsidae (Plate XXIX, 67), and the Agromyzidae (Plate XXXI, 72). Finally, in some families no marked evidence of either suture was to be found, as in the Lonchopteridae (Plate XIX, 31), the Platypezidae (Plate XIX, 33), and the Pipunculidae (Plate XX, 34). Among the species of anthomyids

studied, two of these stages were represented, eight species showing the adventitious suture and the ventral part of the suture separating the first and second tergites, and four species showing only the adventitious suture.

In drawing conclusions regarding any uniformities existing among Diptera in respect to the location of abdominal spiracles, perhaps it would be best to disregard the first and those beyond the fifth segment, and consider only the second, third, fourth, and fifth segments. The integument in which the first abdominal spiracle is located is the most subject to change, as it is just at the point of attachment of the abdomen to the thorax. As there is a necessity for flexibility at this point, the body wall is usually membranous, and as a result the first abdominal spiracle is, with few exceptions, as in the cyrtid (Plate XVI, 23), the lonchopterid (Plate XIX, 31), the tachinid (Plate XXI, 38), the dexiid (Plate XXI, 39), and three species of anthomyids (Plates XXII, 42, and XXIII, 45 and 48), found in membrane. Beyond the fifth segment, the spiracles are so affected by the forces producing the modification of the segments into the genitalia that these too are unreliable. But in considering the second, third, fourth, and fifth spiracles in regard to location in membrane or chitin, some uniformities are seen. All four of these spiracles in each family of the Calyptratae except the Oestridae, in which all are in the membrane, are found in chitin. Among the Acalyptratae, all four spiracles in the Scatophagidae and the Ephydridae, and the third, fourth, and fifth in the Oscinidae, are found in chitin. All other representatives of families have these spiracles in membrane. Aside from these two groups, only scattered cases are found in which these spiracles are surrounded by chitin. In the Cyrtidae, all four are in chitin; in the Lonchopteridae and the Platypezidae, only the third, fourth, and fifth are in chitin.

The pleuro-trochantin (ptn^3) of the metathorax appears as a chitinized sclerite in all the Cyclorrhapha, with the possible exception of the Oestridae (Plate XXI, 37), the Tachinidae (Plate XXI, 38), and the Pipunculidae (Plate XX, 34). Among the Brachycera there seem to be two families showing true chitin in this sclerite, the Asilidae (Plate XVIII, 28) and the Lonchopteridae (Plate XIX, 31). This sclerite appears as membrane or as questionable chitin, if at all, in all other families.

In a few families it was rather difficult to separate the epimeron of the metathorax from the sclerites of the first abdominal segment. These

species sometimes give one the impression that the epimeron of the metathorax is an abdominal sclerite and the first tergite is a thoracic sclerite. Because, for the most part, this confused condition exists among the Brachycera, attention is called to it. This is the case in all the families except the Stratiomyiidae (Plate XV, 19), the Empididae (Plate, XVIII, 30), the Lonchopteridae (Plate XIX, 31), and the Phoridae (Plate XIX, 32).

Perhaps one of the clearest characters that nature has supplied in the area studied, and one on which the whole group of flies can be divided, is the pleural suture of the mesothorax. In the Nemocera with the exception of the Psychodidae, and in the Brachycera with the exception of the Cyrtidae, this suture runs more or less straight from the coxa to the wing process. If it bends forward at all it is on a rather easy curve, but in all the Brachycera of the Orthorrhapha, with the exception of the one cited above, and in all the Cyclorrhapha, this suture takes an abrupt turn cephalad (in some cases the angle is equal to 90° or more) in its course from the leg to the wing area.

Lastly, the writer wishes to call attention to the presence of a tongue-like structure in the membrane of the mesothoracic coxae of all the Calyptratae and the Acalyptratae, with the exception of the Oestridae, and its absence in all other families except the Syrphidae.

These characteristics do not as a whole point to the same places for the division of the order as the one adopted in this paper, or to any other single classification. But there are characters, such as the presence or absence of the adventitious suture and the character of the pleural suture of the mesothorax, which divide rather definitely where they strike and should be of value for that reason. Certainly this investigation has emphasized the fact that the last word has not been said on the systematic position of some members in such families as the Cyrtidae, the Oestridae, the Scatophagidae, the Ephydridae, the Oscinidae, and a number of others whose study has offered obstructions to uniformities within a time-honored system.

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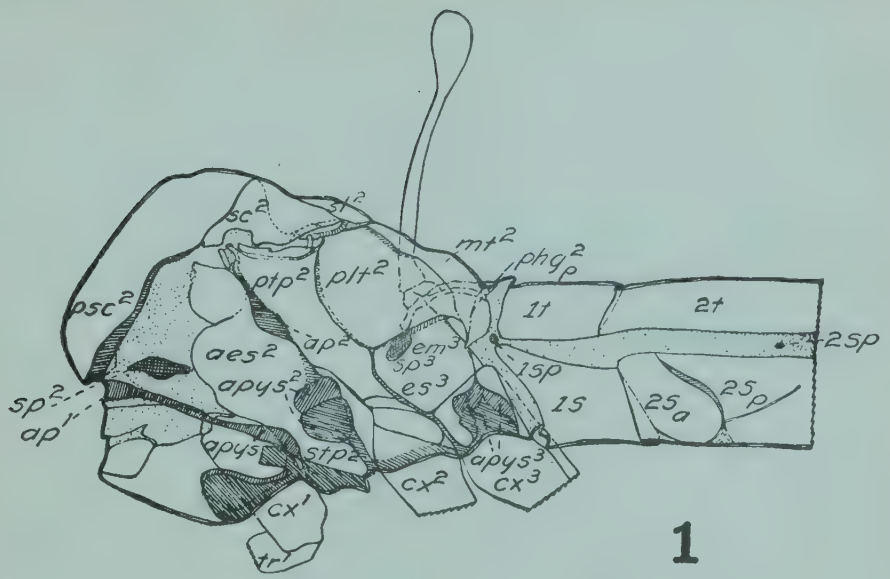
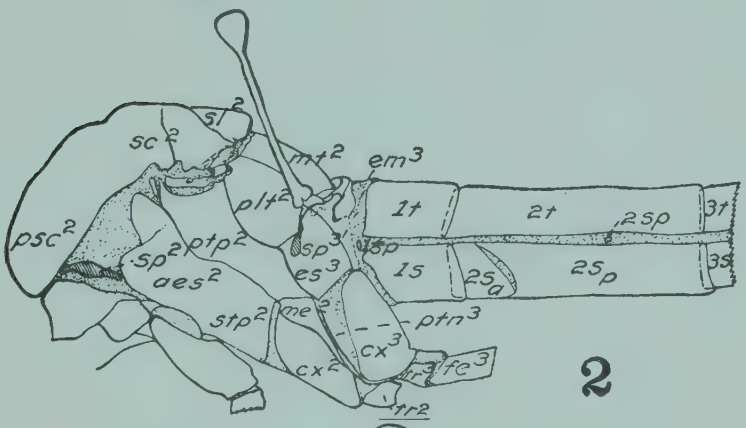
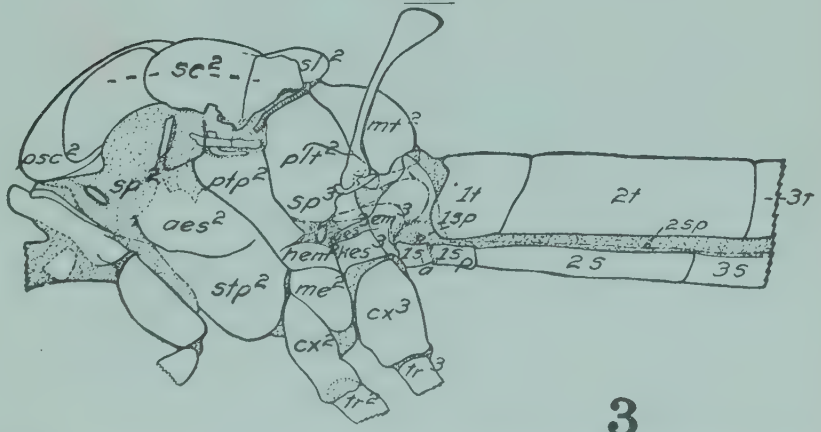
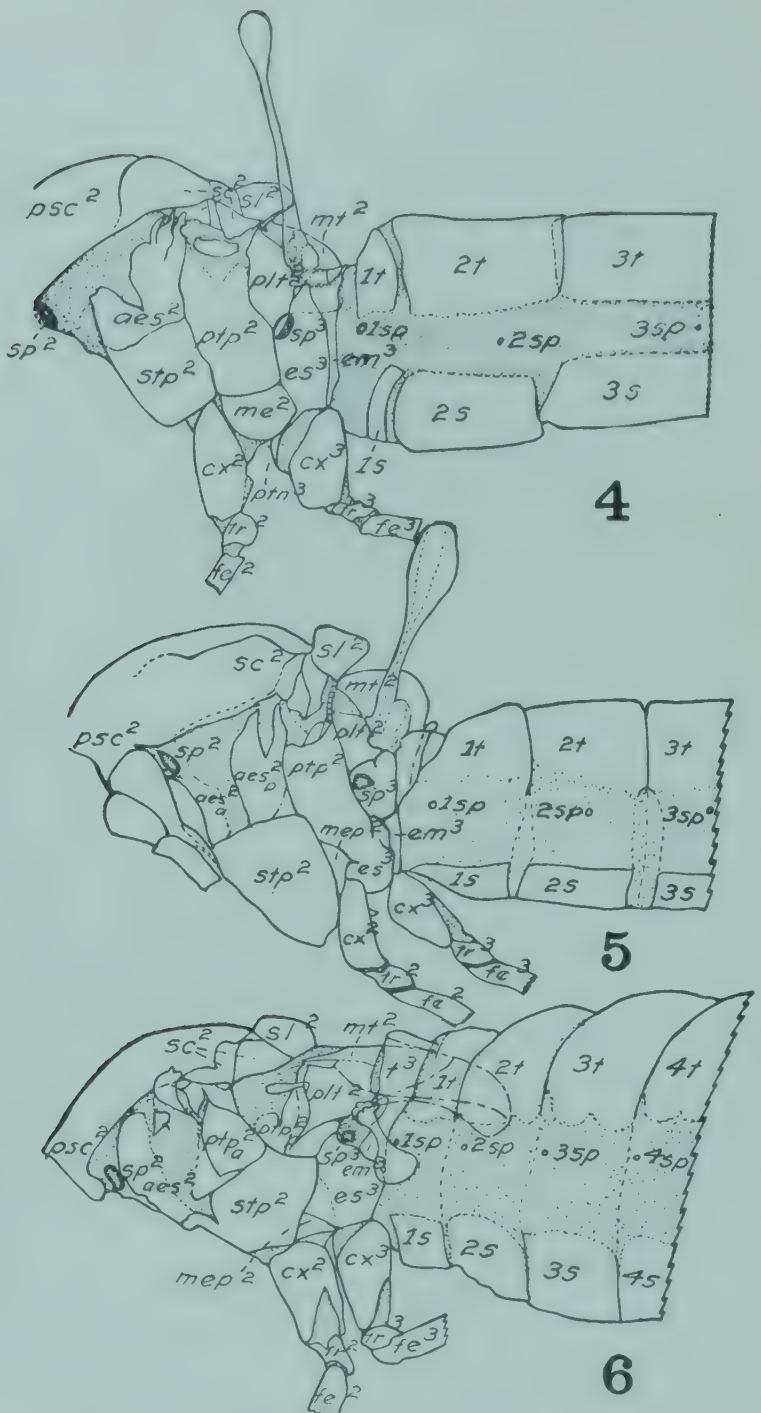


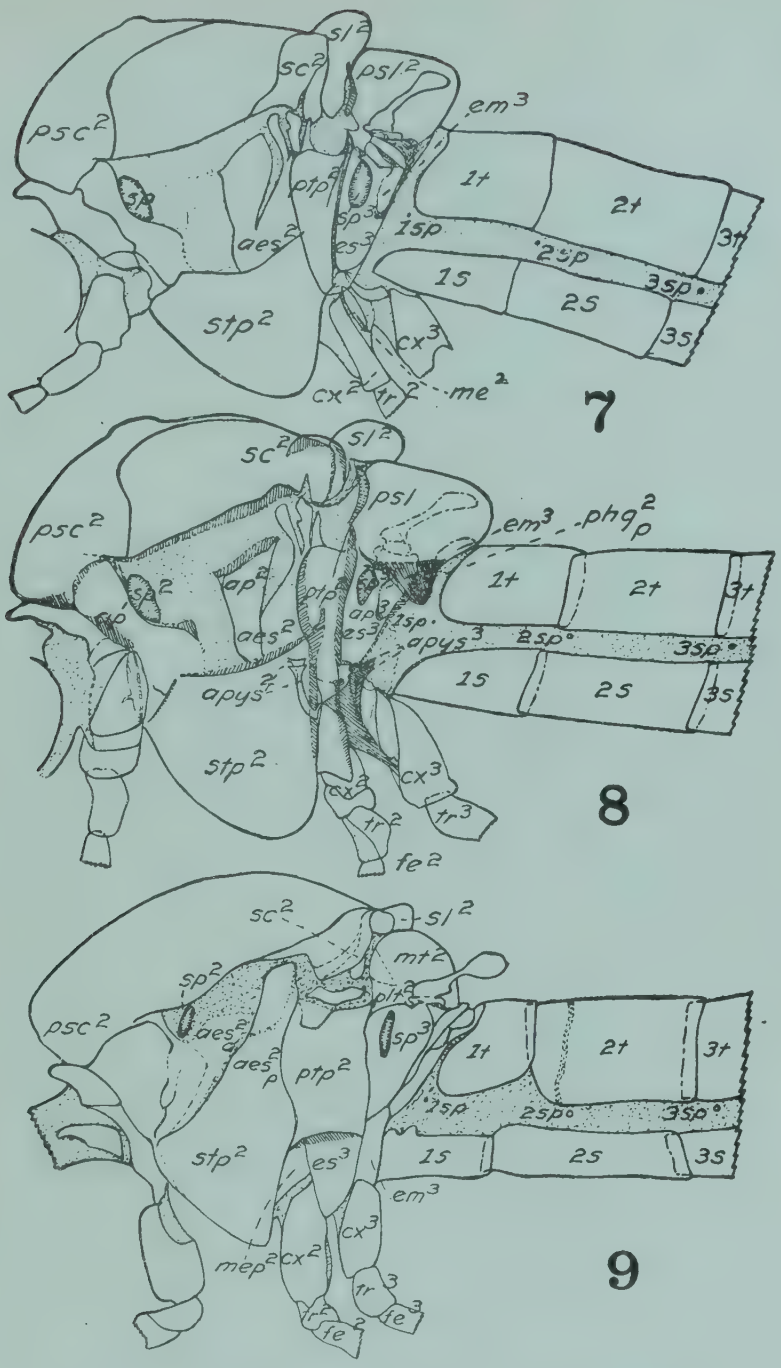




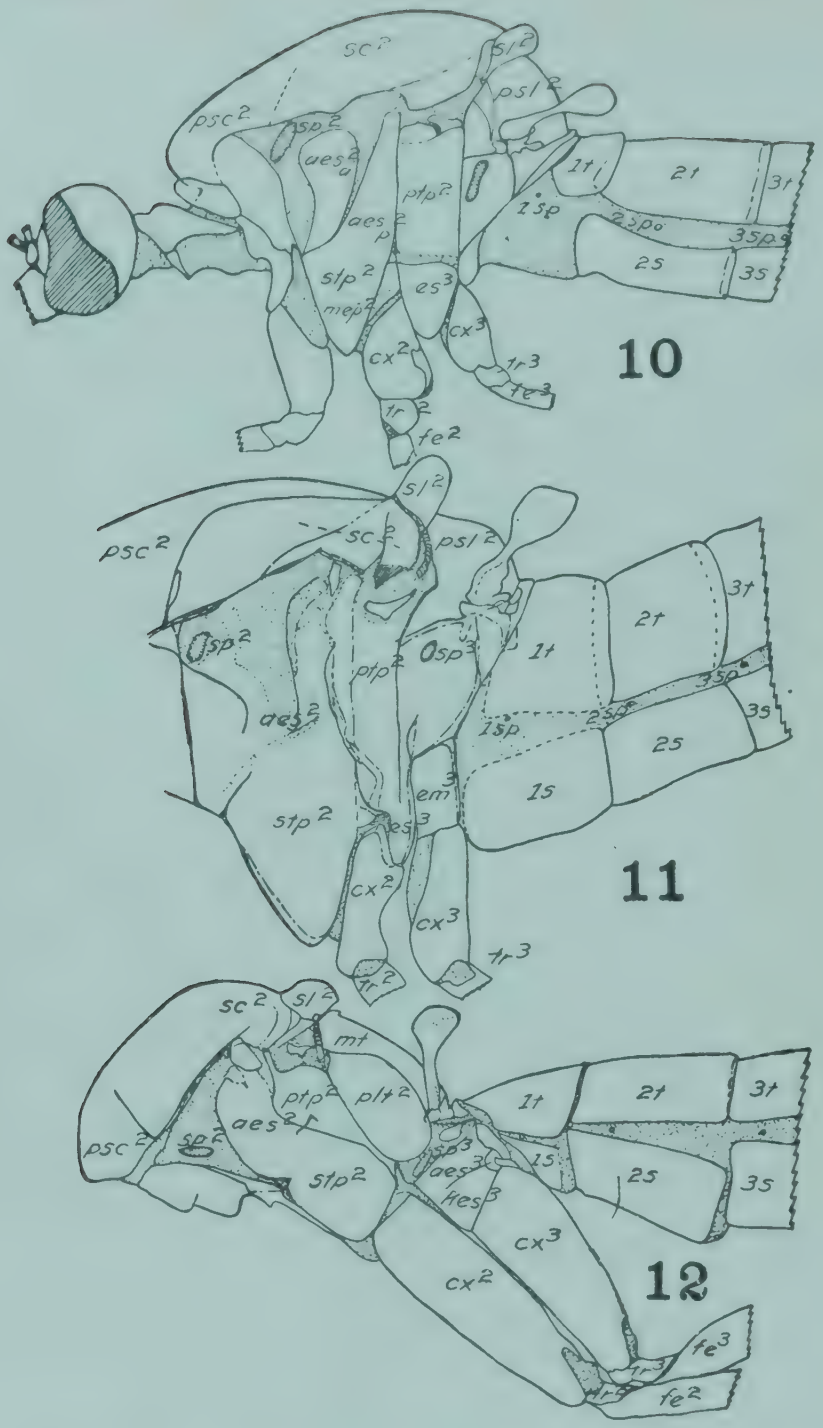
1, *Pedicia albivitta*, female (Tipulidae); internal view, showing endothorax. 2, *Pedicia albivitta*, female (Tipulidae). 3, *Pachyrrhina ferruginea*, male (Tipulidae)



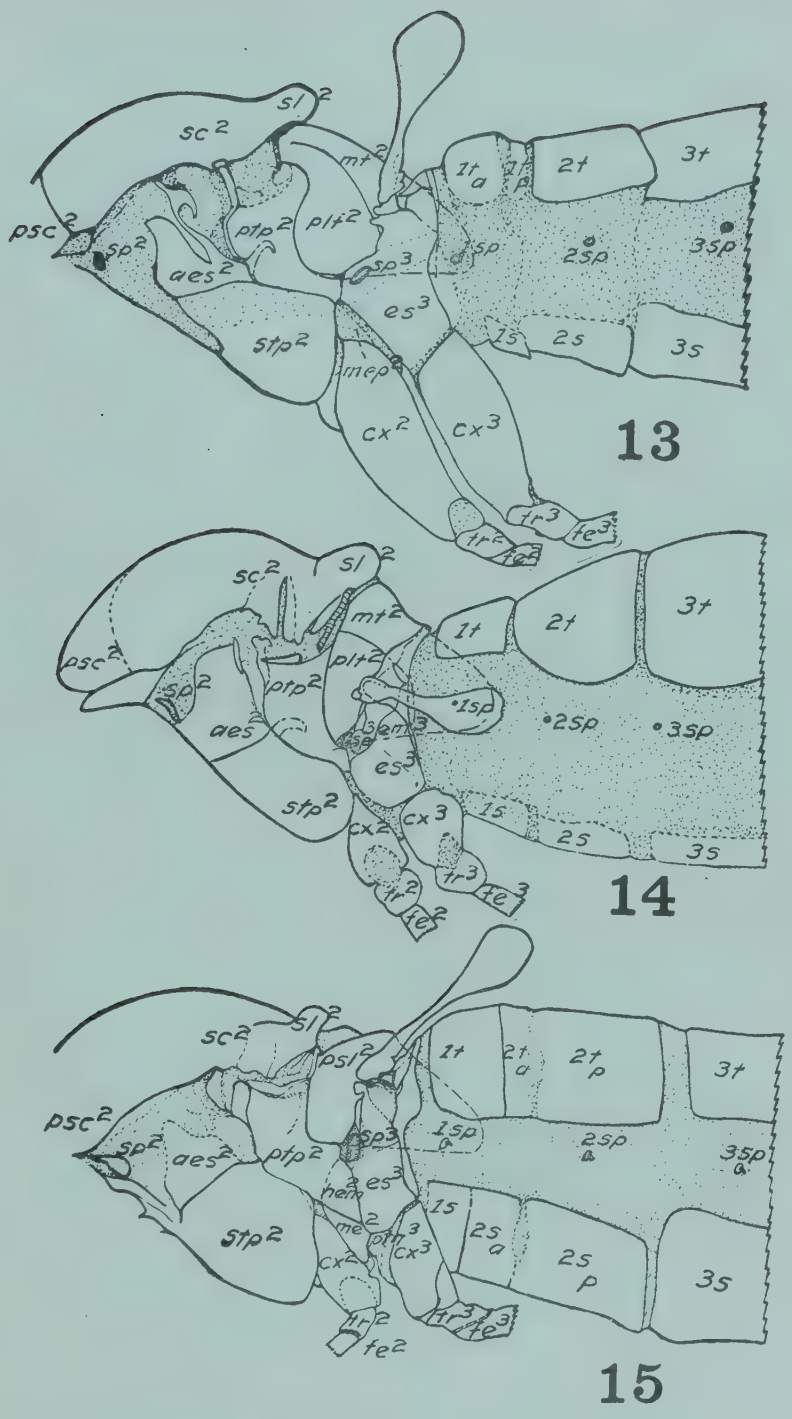
4, *Trichocera brumalis*, female (Rhyphidae). 5, *Dixa modesta*, female (Dixidae). 6, *Psychoda slossoni*, female (Psychodidae)



7, *Chironomus ferrugineavitta*, male (Chironomidae). 8, *Chironomus ferrugineavitta, male* (Chironomidae); internal view, showing endothorax. 9, *Culex canadensis*, male (Culicidae)



10, *Anopheles quadrimaculata*, female (Culicidae). 11, *Corethra albipes*, female (Culicidae). 12, *Leia winthemi*, female (Mycetophilidae)



13, *Sciara ochrolabis*, male (Sciaridae). 14, *Rhabdophaga strobiloides*, male (Cecidomyiidae). 15, *Plecia heteroptera*, female (Bibionidae)

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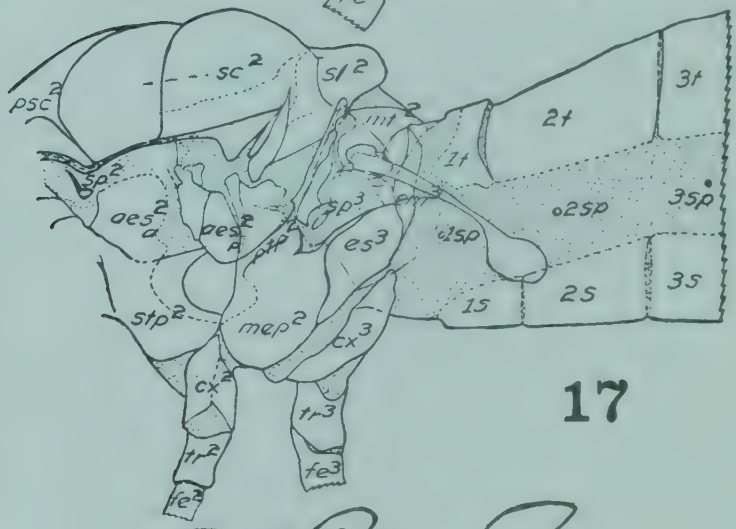

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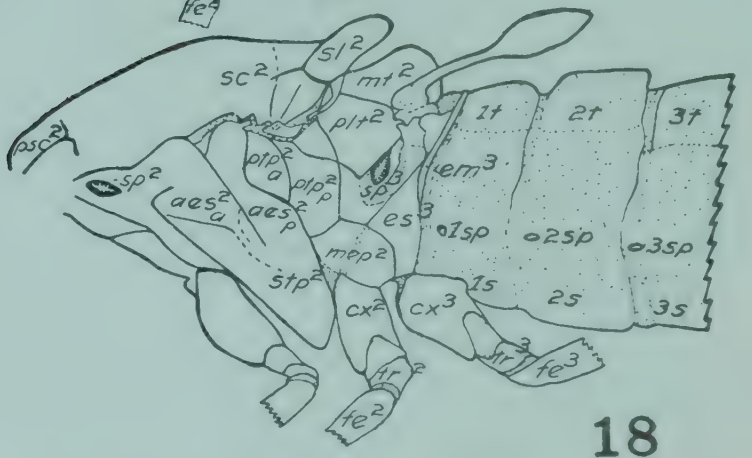

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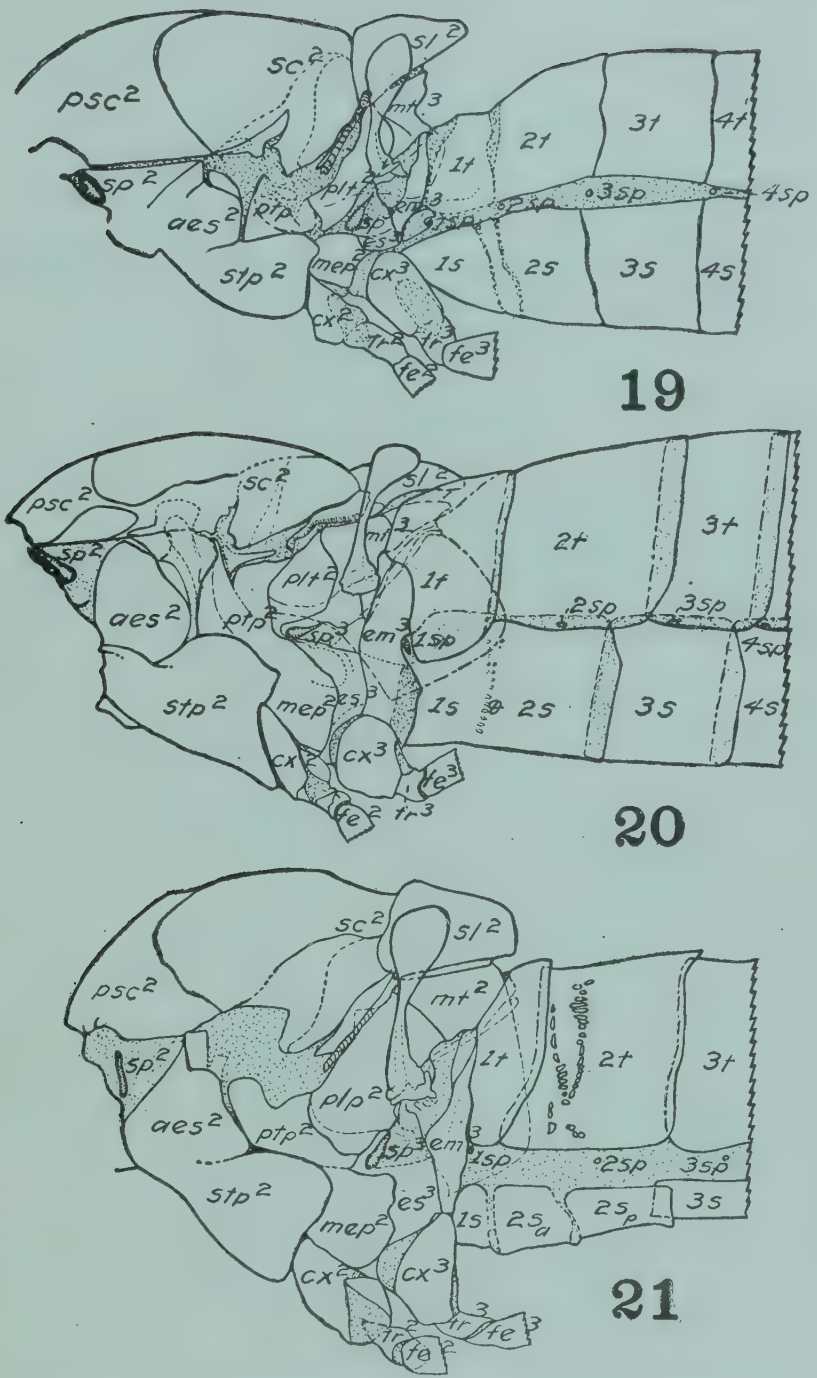
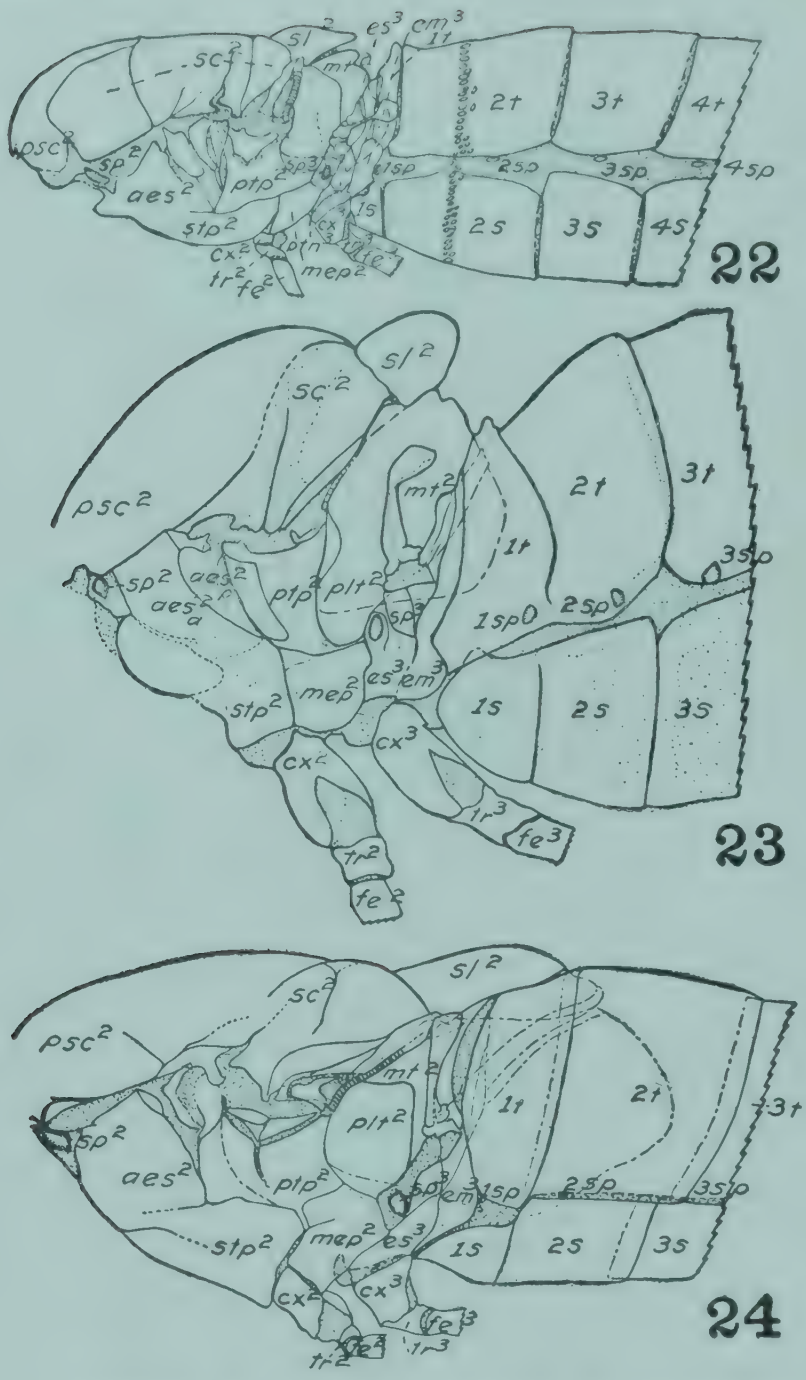
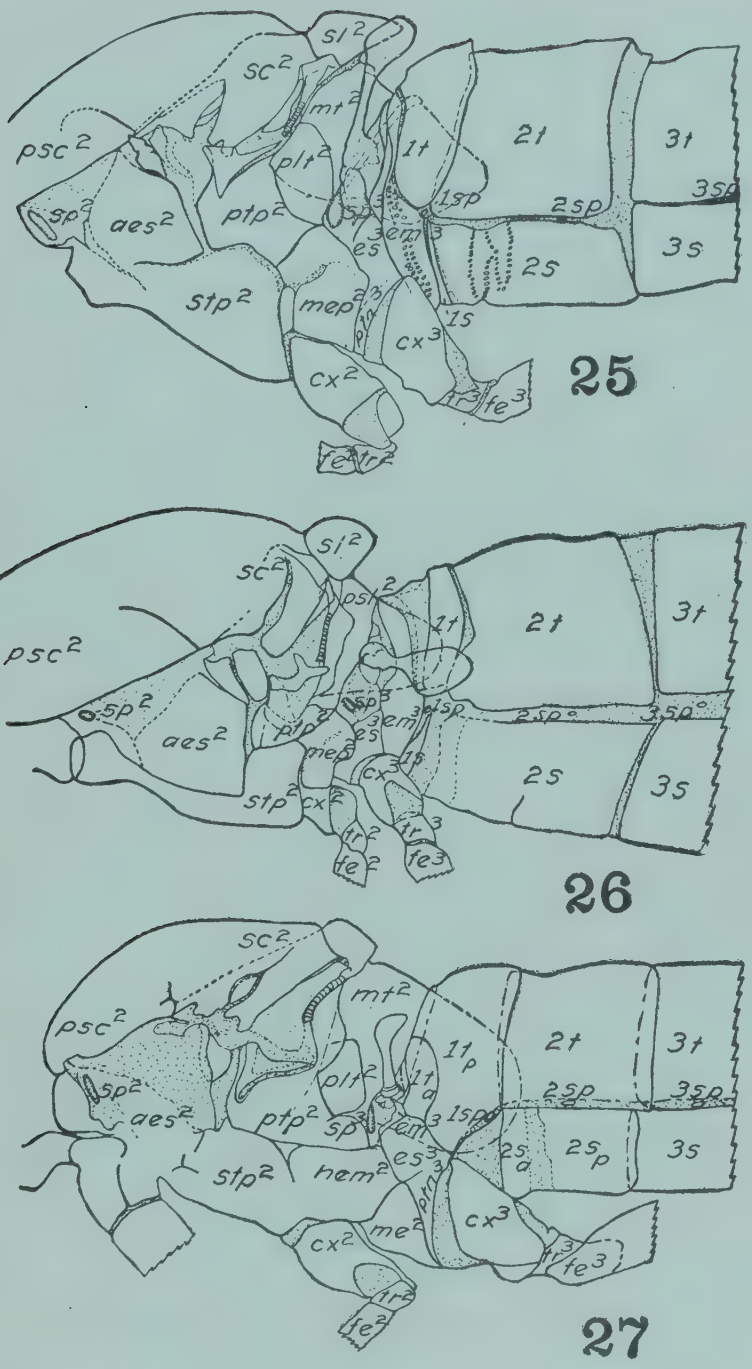
16, ***Simulium hirtipes,*** male (Simuliidae). **17,** ***Blepharocera tenuipes,*** female (Blepharoceridae). 18, *Orphnephila americana*, female (Orphnephilidae)



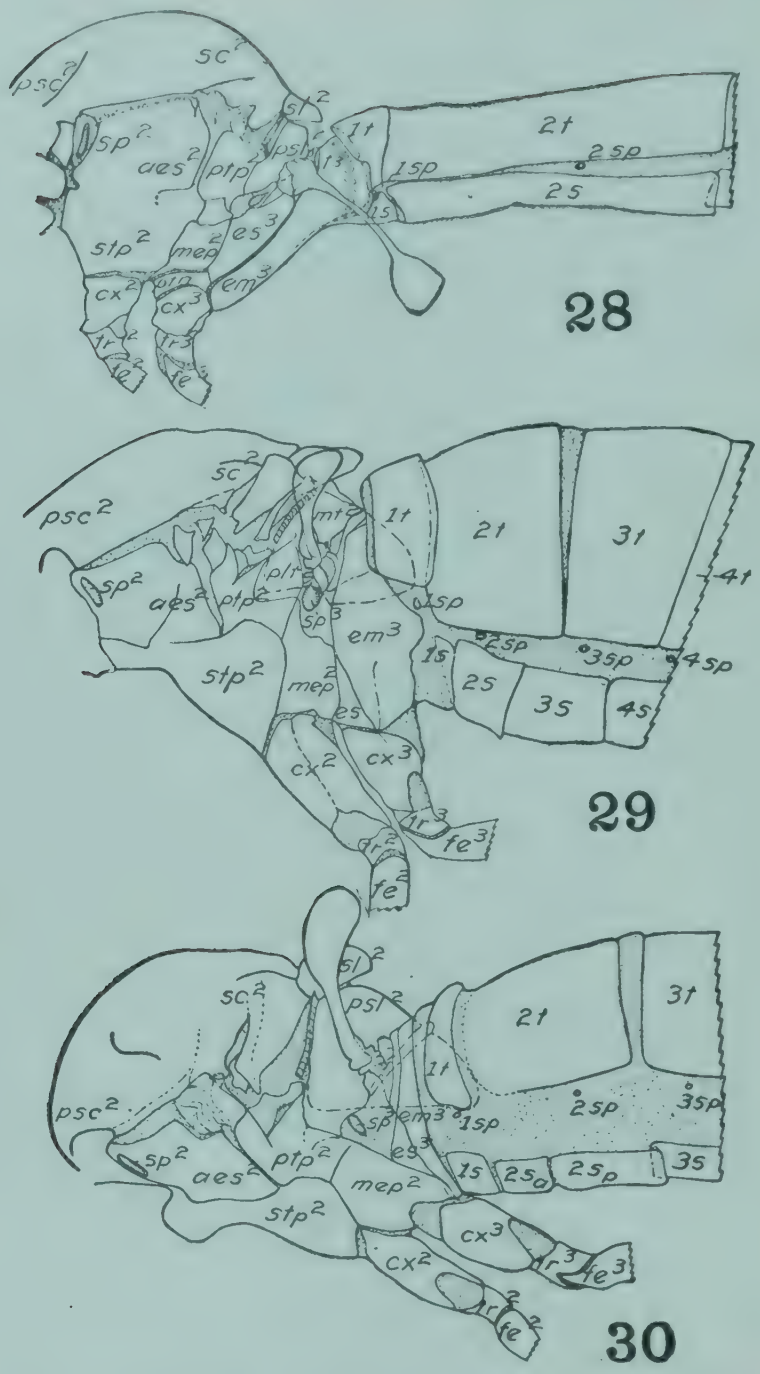
19, *Allognosta fuscitarsis*, female (Stratiomyiidae). 20, *Chrysops indus*, male (Tabanidae). 21, *Chrysopila ornata*, male (Leptidae)



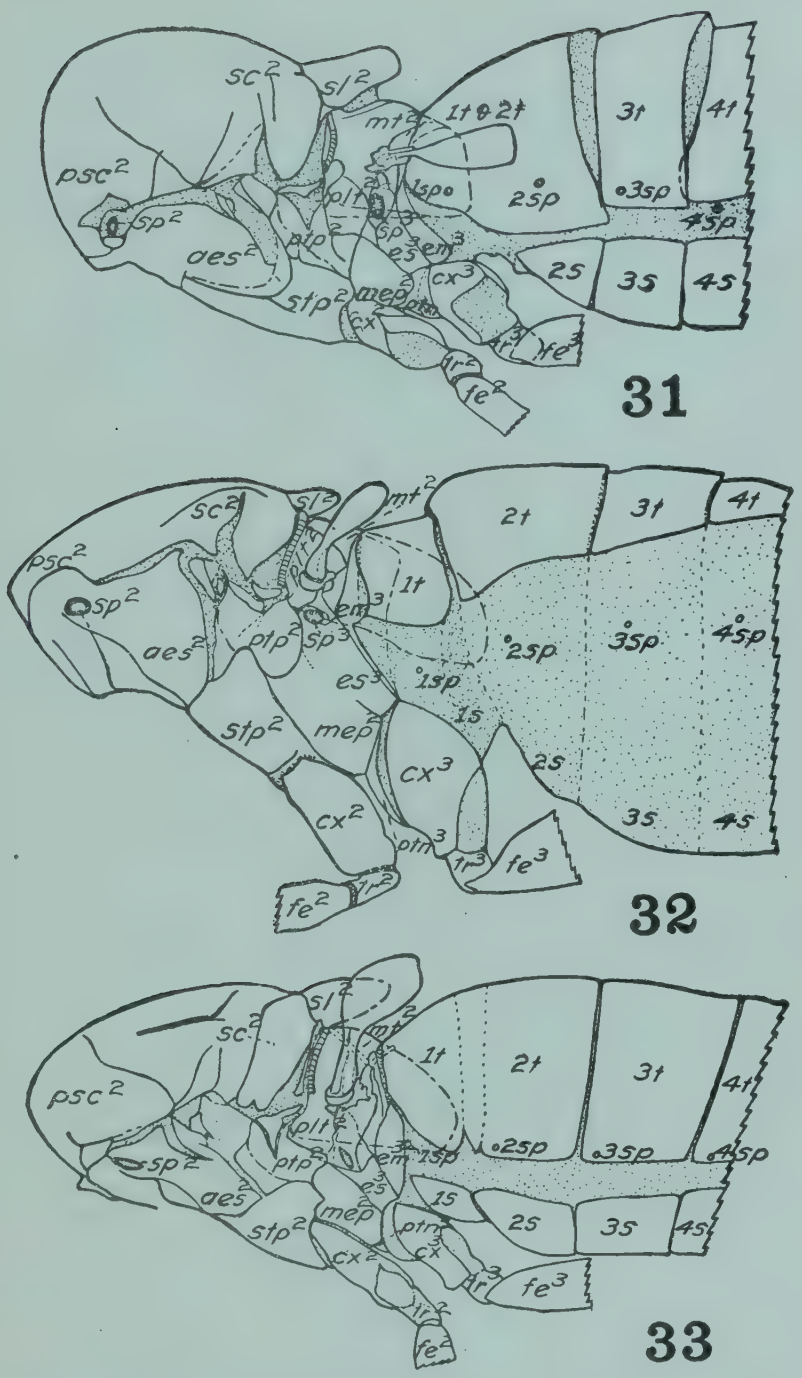
22, *Hirmoneura* sp., female (Nemistrinidae). 23, *Oncodes incultus*, female (Cyrtidae). 24, *Anthrax alternata*, female (Bombylidae)



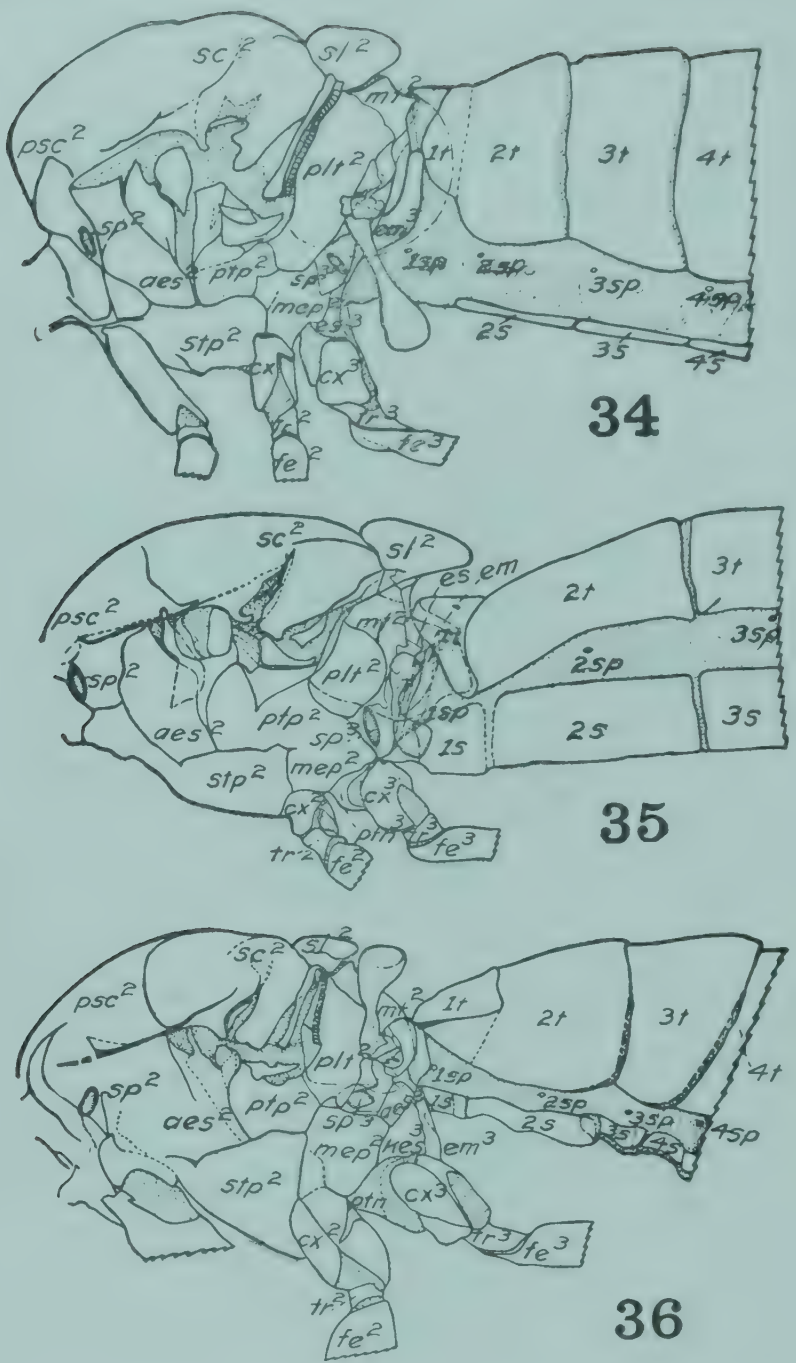
25, *Thereva fucata*, male (Therevidae). 26, *Scenopinus fenestralis*, female (Scenopinidae). 27, *Midas clavatus*, female (Midaidae)



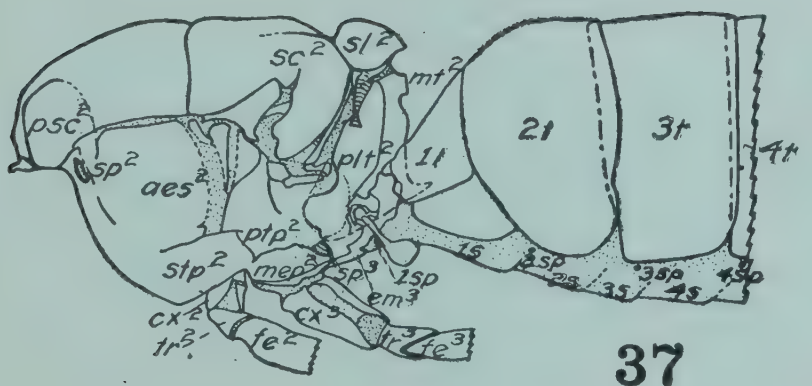
28, *Leptogaster loewi*, female (Asilidae). 29, *Dolichopus cuprinus*, male (Dolichopodidae). 30, *Rhamphomyia* sp., female (Empididae)

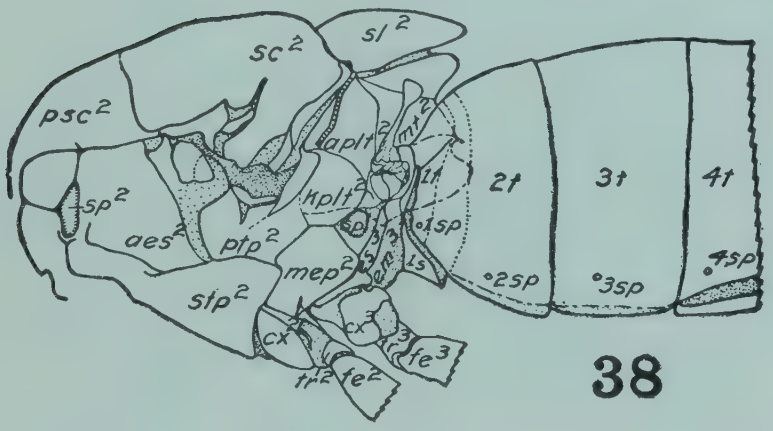


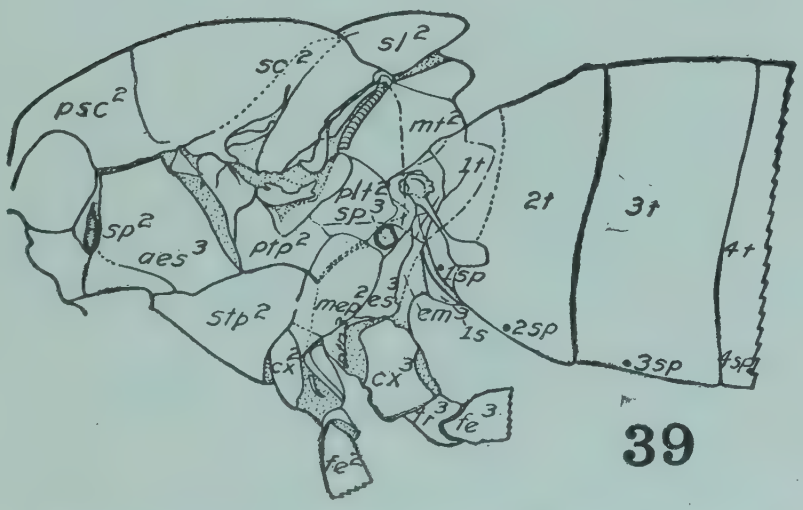
31, *Lonchoptera* sp., female (Lonchopteridae). 32, *Phora concinna*, female (Phoridae). 33, *Platypeza velutina*, female (Platypezidae)



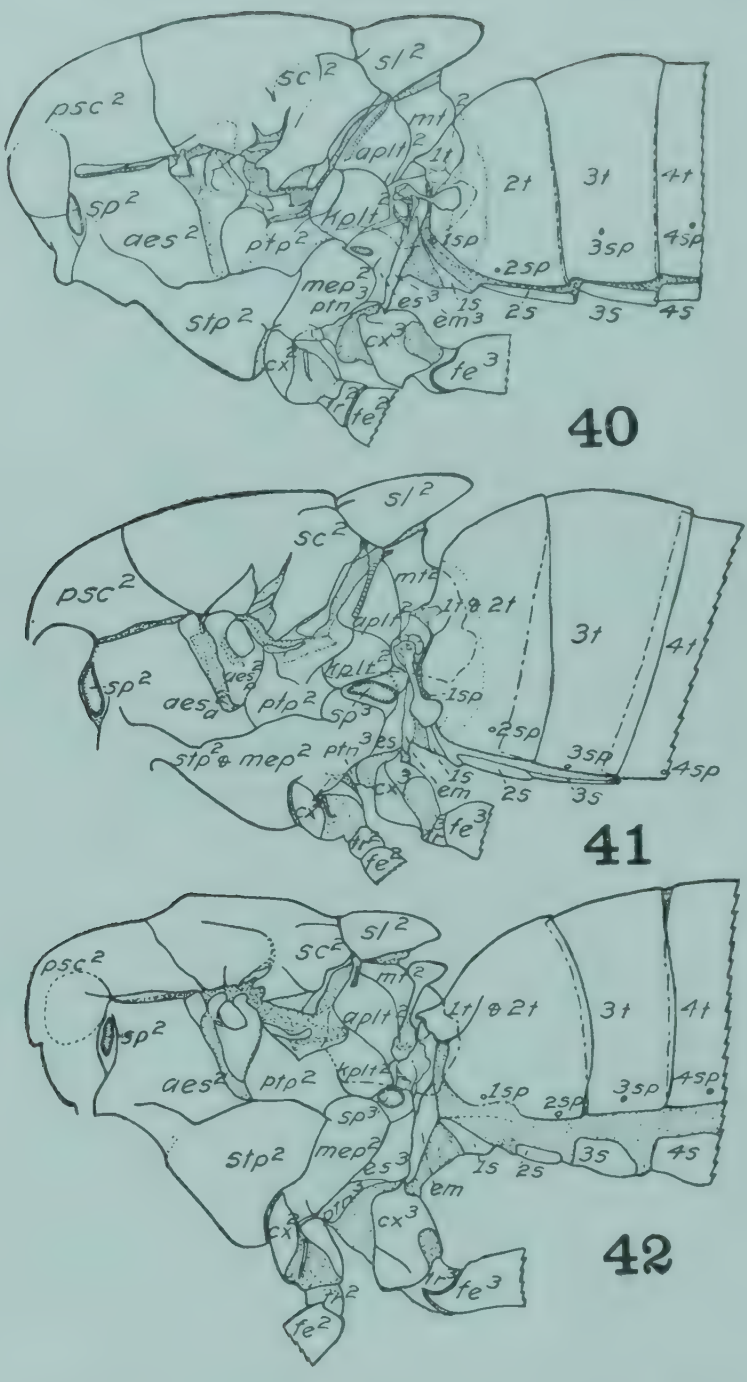
34, *Pipunculus atlanticus*, female (Pipunculidae). 35, *Syrphus americanus*, male (Syrphidae). 36, *Myopa vesiculosa*, male (Conopidae)



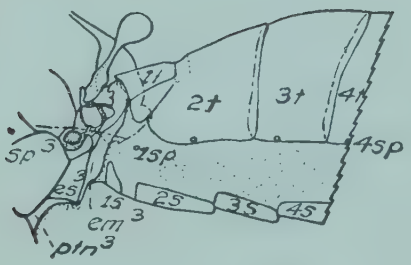




37, *Gastrophilus intestinalis*, female (Oestridae). 38, *Tachina mella*, female (Tachinidae). 39, *Thelaira nigripes*, male (Dexiidae)



40, *Sarcophaga communis*, male (Sarcophagidae). 41, *Muscina stabulans*, female (Muscidae). 42, *Macrorchis ausoba*, male (Anthomyiidae)



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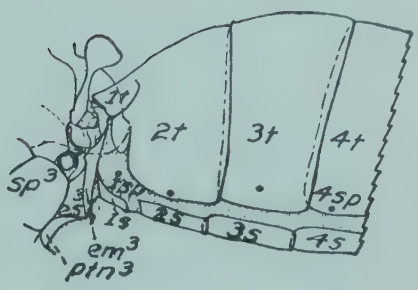

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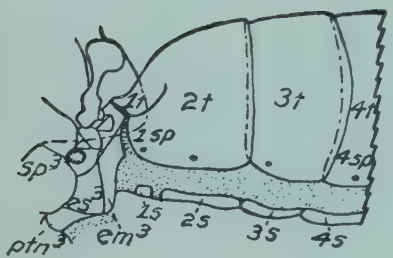

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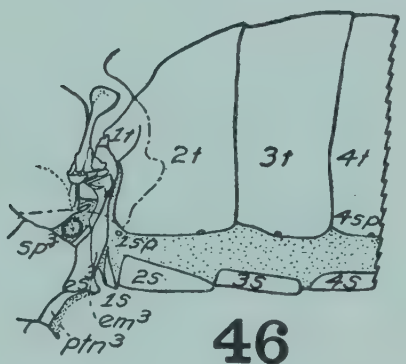

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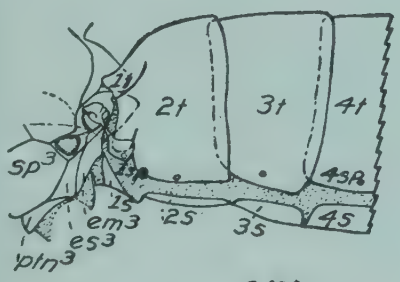

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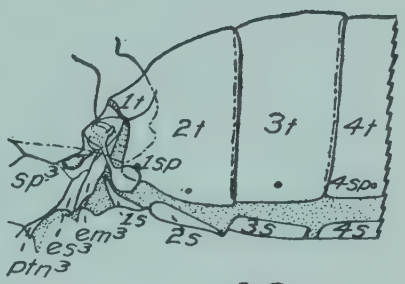

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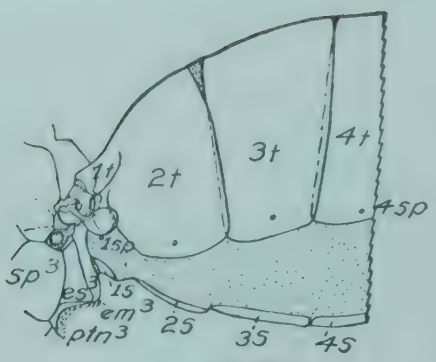
43, *Chortophila cilicrura*, male (Anthomyiidae). 44, *Hylephila paludis*, female (Anthomyiidae). 45, *Schoenomyza dorsalis*, female (Anthomyiidae). 46, *Ophyra leucostoma*, male (Anthomyiidae). 47, *Lispa sociabilis*, female (Anthomyiidae). 48, *Limnophora aequifrons*, male (Anthomyiidae)



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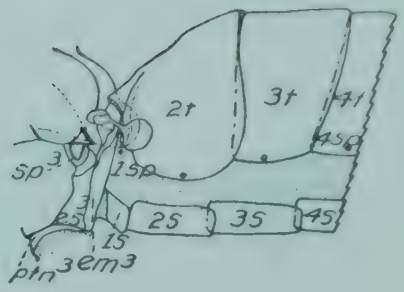

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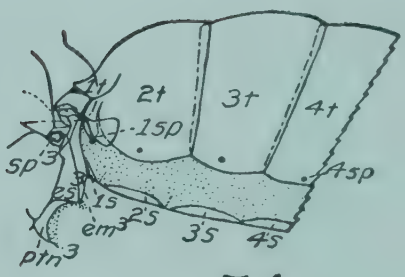

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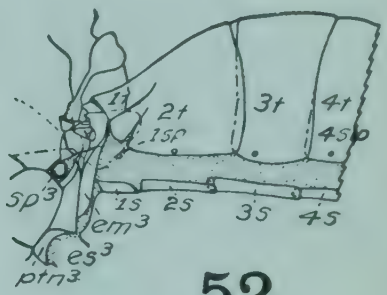

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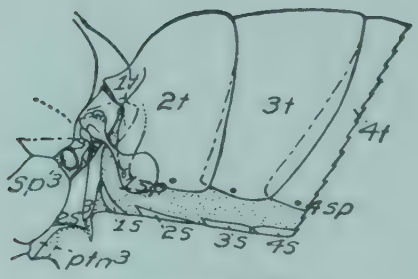

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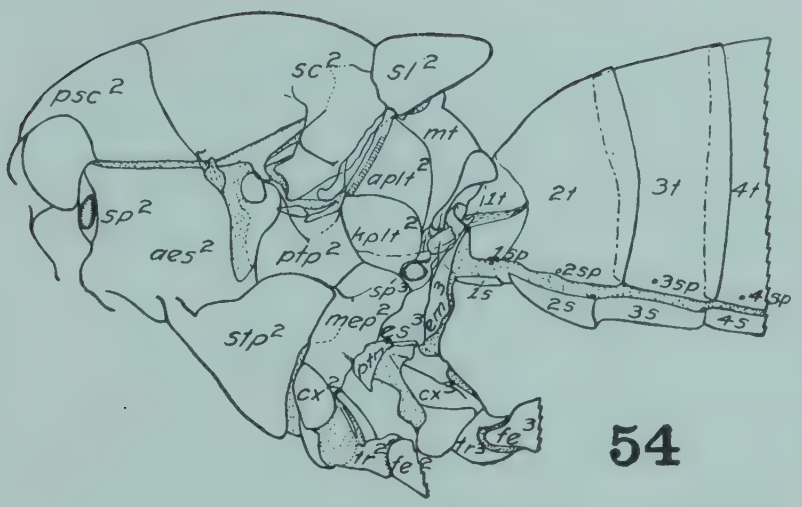
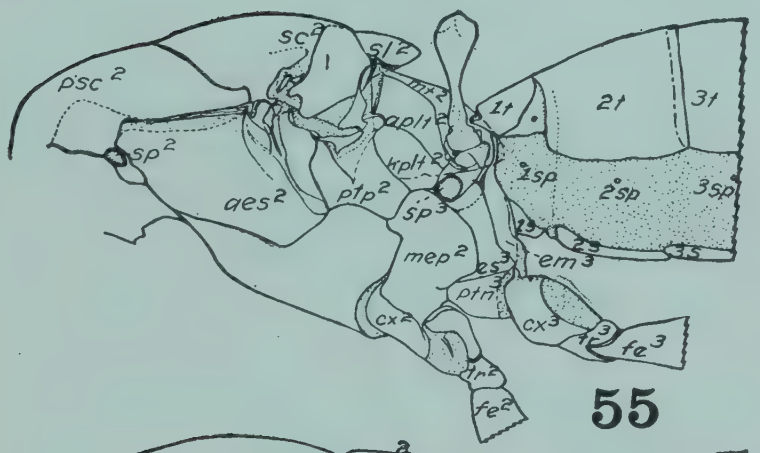
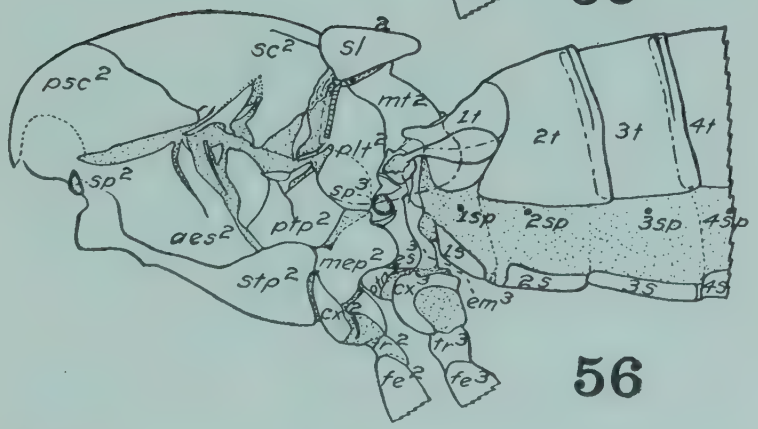
49, *Eremomyia cylindrica*, female (Anthomyiidae). 50, *Pegomyia affinis*, female (Anthomyiidae). 51, *Hylemyia lipsia*, female (Anthomyiidae). 52, *Anthomyia radicum*, male (Anthomyiidae). 53, *Hebecnema umbratica*, female (Anthomyiidae)







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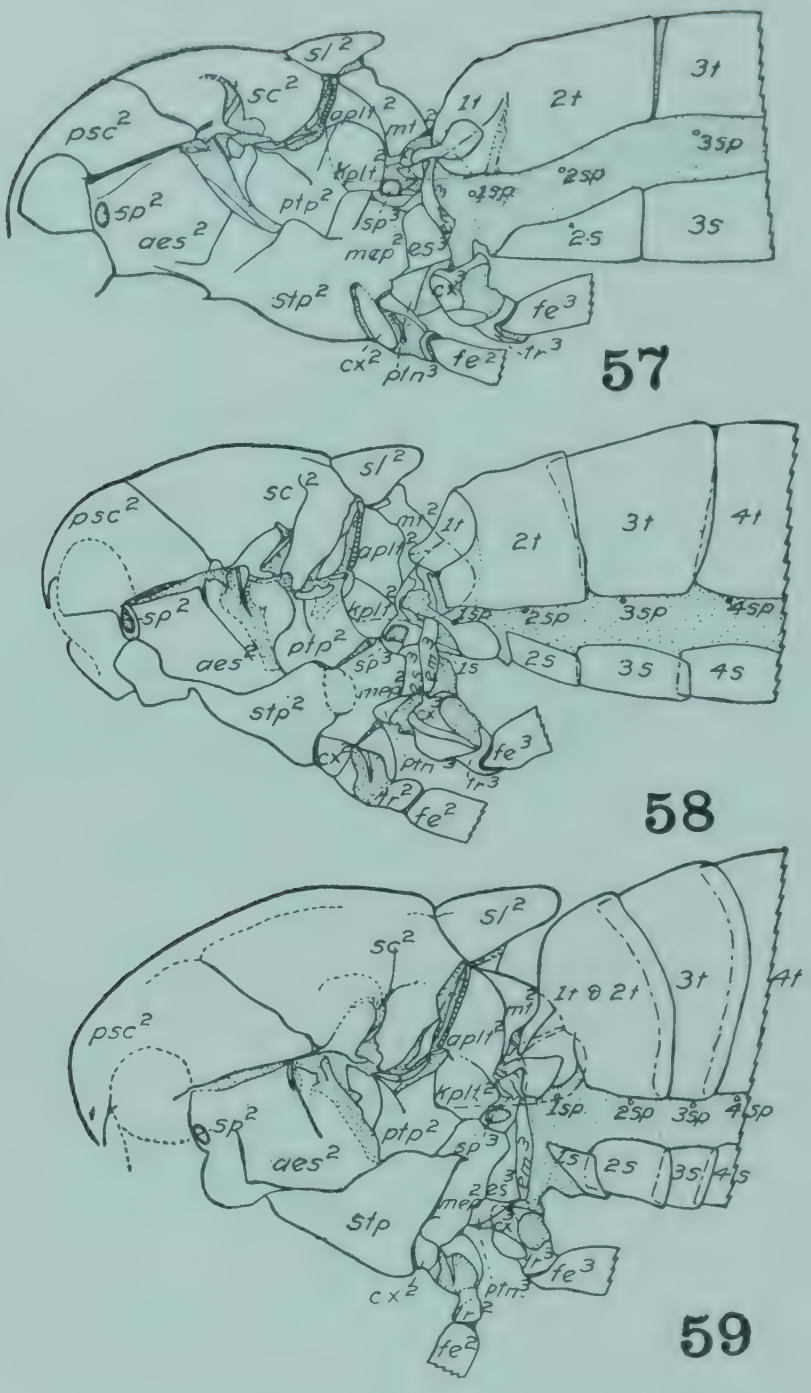
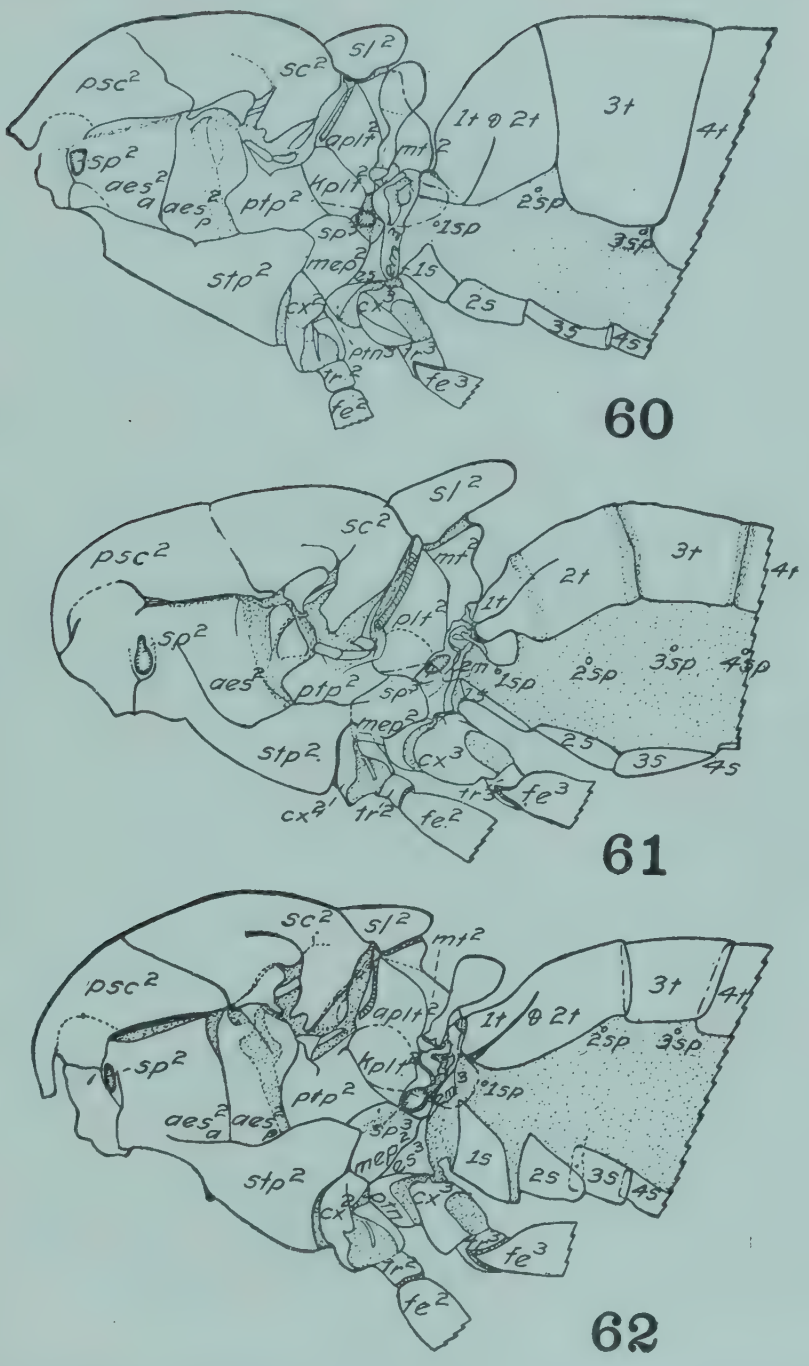
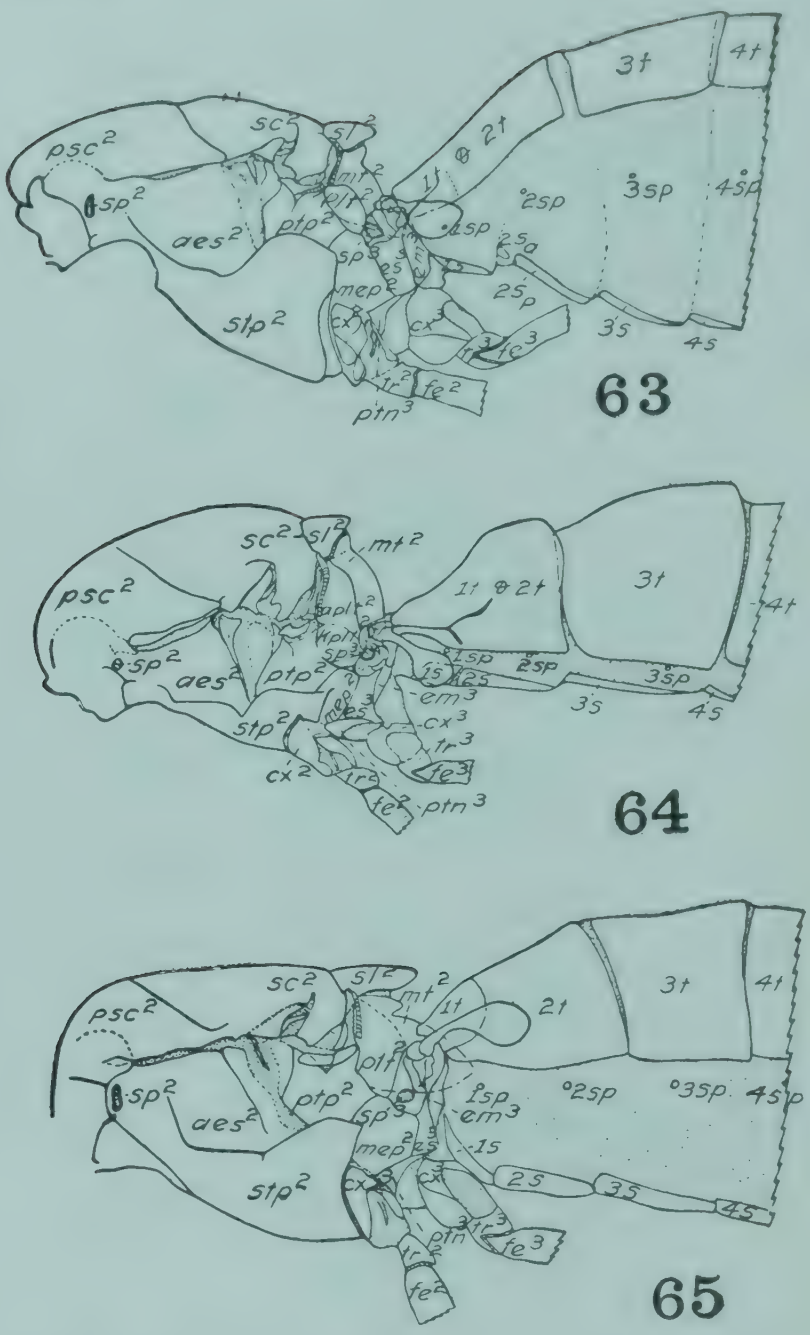


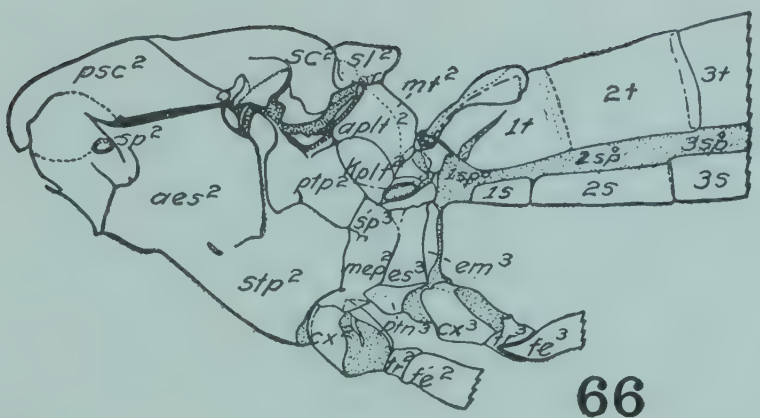
57, *Borborus equinus*, female (Borboridae). 58, *Dictya umbrarum*, female (Sciomyzidae). 59, *Sapromyza lupulina*, male (Sapromyzidae)



60, *Rivellia viridulans*, female (Ortalidae). 61, *Rhopalomera flaviceps*, female (Rhopalomeridae). 62, *Euaresta festiva*, female (Trypetidae)



63, *Calobata albiceps*, female (Micropezidae). 64, *Sepsis violacea*, female (Sepsidae). 65, *Piophila casei*, female (Piophilidae)



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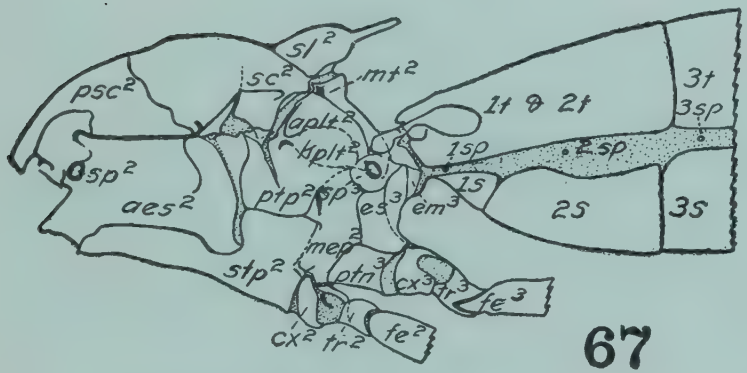

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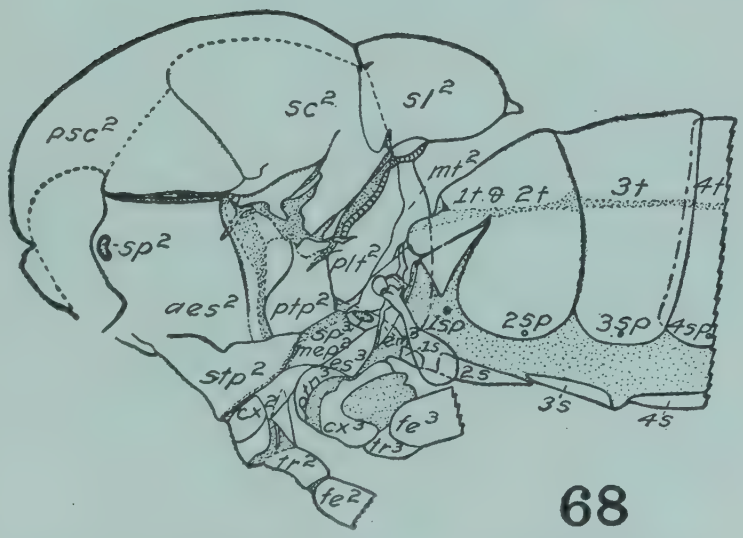

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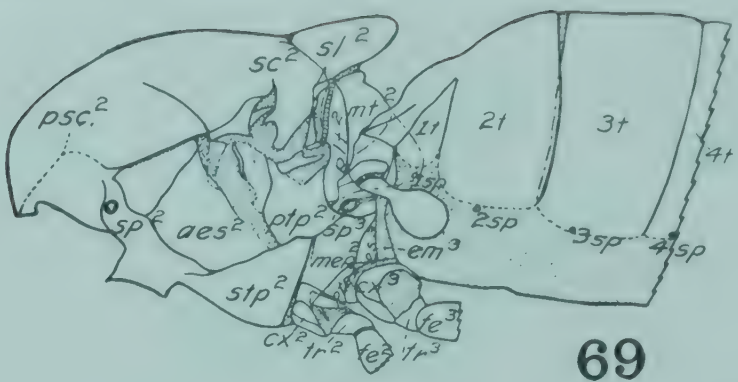
66, *Loxocera pleuritica*, male (Psilidae). 67, *Sphyracephala brevicornis*, female (Diopsidae). 68, *Parydra limpidipennis*, female (Ephydridae)



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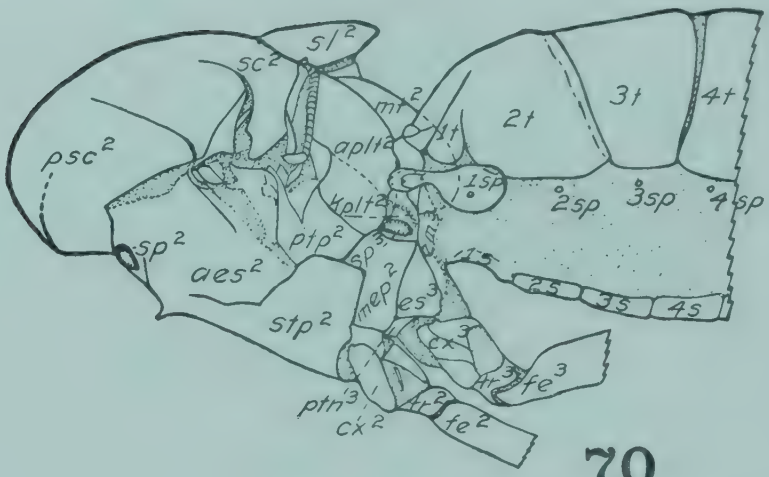

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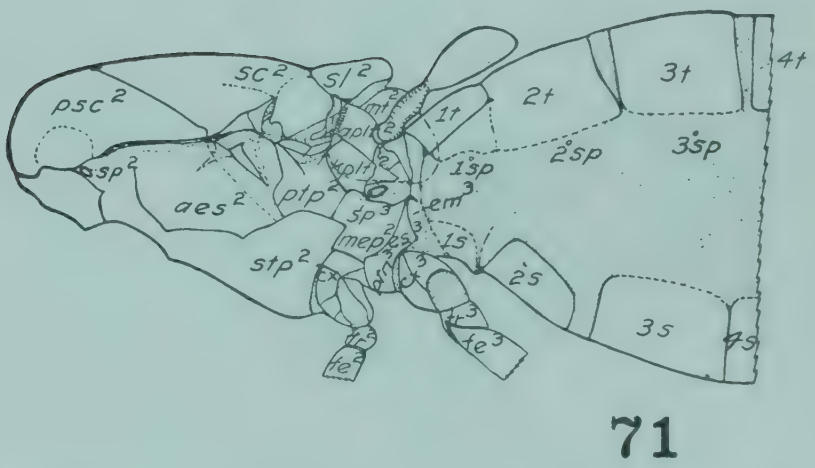

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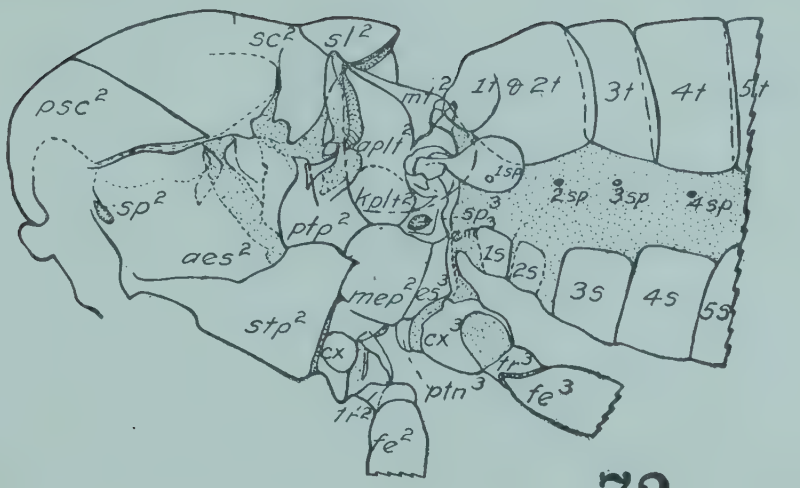
69, *Chlorops* sp., male (Oscinidae). 70, *Drosophila melanogaster* (?), female (Drosophilidae). 71, *Anthomyza gracilis*, female (Geomyzidae).



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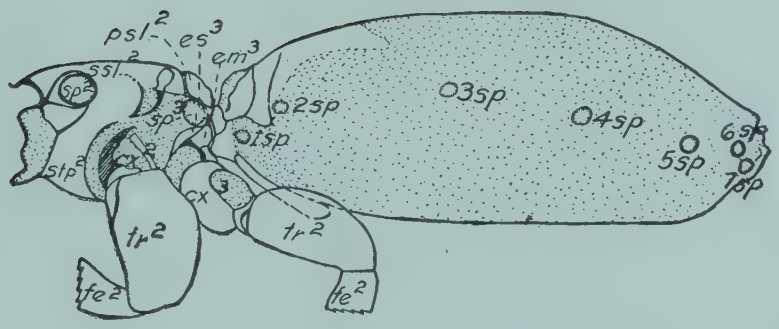

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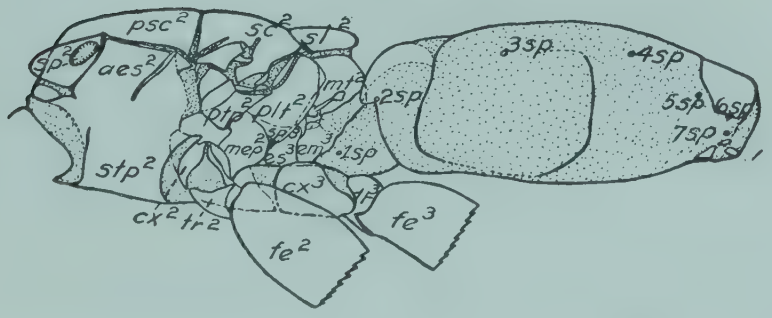

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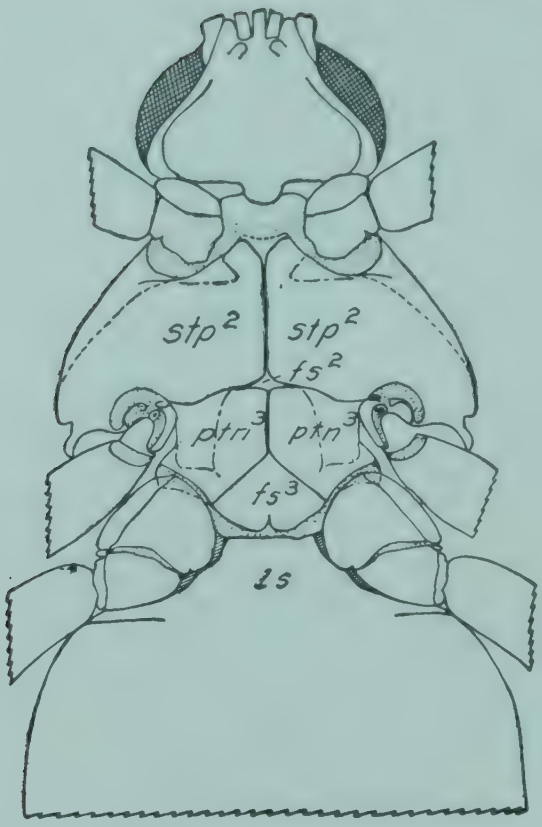
72, *Agromyza lateralis*, male (Agromyzidae). 73, *Melophagus ovinus*, female (Hippoboscidae). 74, *Olfersia americana*, female (Hippoboscidae)



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75, *Olfersia americana*, female (Hippoboscidae); ventral view.
76, *Panorpa venosa*, female (Panorpidae)

AUGUST, 1921 MEMOIR 45

CORNELL UNIVERSITY
AGRICULTURAL EXPERIMENT STATION

THE BOTRYTIS BLIGHT OF TULIPS

EDWIN F. HOPKINS

ITHACA, NEW YORK
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CONTENTS

PAGE

The host plants 315
Varietal susceptibility 316
The disease 316
Names 316
History and distribution 317
Economic importance 318
Symptoms 319
On the bulbs 319
On the leaves 323
On the flowers 326
On the stalks 328
Etiology 328
Nomenclature 328
Morphology 332
Physiology 335
Growth 335
Conidia production 338
Dissemination of conidia 339
Pathogenicity 339
Experimental methods 340
Results of inoculations 342
Discussion of parasitism 349
Life history 350
Primary inoculation and infection 350
Secondary inoculations and infections 350
Pathological histology 351
Control 355
Summary 357
Bibliography 359

THE BOTRYTIS BLIGHT OF TULIPS

TULIP PLANT AFFECTED WITH BOTRYTIS BLIGHT

One-half natural size

THE BOTRYTIS BLIGHT OF TULIPS[1]

EDWIN F. HOPKINS

THE HOST PLANTS

It is reasonably certain that the Botrytis blight is restricted to plants in the genus Tulipa. This genus includes *Tulipa Gesneriana* L., the Darwin, or late, tulips, *T. suaveolens* Roth., the Duc van Thol tulip, embracing the early and forced varieties, and *T. sylvestris* L., the so-called wild tulip. The members of this genus have been under cultivation for so long that it is difficult to refer them to any natural species although the arrangement just given is commonly accepted (Bailey, 1917:3393-3394).[2]

Numerous references to the occurrence of this disease on other hosts have appeared in the literature. However, most of these statements are based on insufficient evidence, and show that the author had under consideration another Botrytis disease and did not attempt to verify his conclusions by cross inoculations. Ritzema Bos (1903a:20), for instance, says that while the disease affects other bulbs, such as hyacinths, gladioli, and certain iris species, the tulip is by far the most susceptible. Klebahn (1905:15-17) takes exception to this statement since he has found the disease on none of these plants except the tulip; furthermore, his experiments show the hyacinth to be immune. He seems to infer that Ritzema Bos was confusing two different diseases, and that possibly, on these hosts, the disease with which he was dealing was caused by *Sclerotium Tuliparum* Klebahn. However, Klebahn states that practical gardeners have told him that on ground which had borne bulbous begonias and dicentra no tulips came up.

Other notes frequently appear by authors who evidently confuse diseases caused by other species of Botrytis with the one under consideration, which is caused by *Botrytis Tulipae* (Lib.) comb. nov. Halsted (1891:352) gives a good example of this in attributing the disease on onions to this organism.

---

[1] Also presented to the Faculty of the Graduate School of Cornell University, March, 1920, as a major thesis in partial fulfillment of the requirements for the degree of doctor of philosophy.

ACKNOWLEDGMENT. The author wishes to express his thanks to Professor H. H. Whetzel, of Cornell University, for his many valuable suggestions and for his helpful advice during the progress of the work.

[2] Dates in parenthesis refer to *Bibliography*, pages 359 to 361.

In order to gain some knowledge of the host range of the parasite concerned, numerous cross-inoculations were made by the writer. These experiments, which are summarized under the heading *Pathogenicity* (page 339), prove that the organism concerned does not attack certain of these hosts under artificial conditions, and therefore it probably would not under natural ones. Klebahn (1904, 1905, 1907) had previously made certain cross-inoculations tending to disprove the existence of a generalized type of parasitism in this pathogene.

The disease is restricted, under normal conditions, to the genus Tulipa; and while similar Botrytis diseases occur on the other hosts mentioned, and even on the tulip itself, they are not identical with this one.

VARIETAL SUSCEPTIBILITY

Varieties of both the early tulips, *Tulipa suaveolens*, and the late tulips, *T. Gesneriana*, are susceptible. Likewise, as already mentioned, the wild tulip, *T. sylvestris*, has been proved susceptible. The writer has collected diseased specimens of many varieties of the first two species and has seen the disease on the wild species.

Klebahn (1905:11), in his experiments, tested five varieties of tulips, presumably early varieties, but finding all susceptible he drew no general conclusion from this result. He thinks it would be desirable to compare the susceptibility of the early and the late species.

The writer found the disease on a large number of varieties of both species, and isolated the causal organism; he also succeeded in artificially infecting both species. He had almost concluded that there was not much difference in susceptibility. But in the spring of 1917, in a garden on the Cornell University campus where there was then a severe outbreak of the disease, one variety of late tulips (Baronne de la Tonnaye), which had certainly been exposed to the infection, showed no evidence of the disease. Up to the present time there has not been an opportunity to test this variety further.

THE DISEASE

NAMES

Various names have been applied to the disease. Ritzema Bos (1903a: 19) incorrectly used the name *kwaden plekken*, a term applied by Dutch bulb growers to soil that will not produce tulips. Later Klebahn (1907:3)

showed that there are various causes of these "bad spots," but that usually they are due to *Sclerotium Tuliparum*. Hence the term *kwaden plekken* may not be applied specifically to this disease.

Ritzema Bos (1903a:19) uses also the word *Umfallen* to designate the disease as it occurs on tulip tops because it often causes the stem to break over. The writer believes, however, that this name is better applied to a physiological disease of tulips described by Sorauer (1903:265). "Tulip mould" is the term used by Massee (1899:158) and also by Halsted (1902:438). Later Jacob (1912) states that it is commonly known as "fire."

The writer would suggest the name *Botrytis blight* for this disease, since it causes a typical blight, and although there is another Botrytis disease of tulips, this is the more important one by far.

HISTORY AND DISTRIBUTION

The Botrytis blight of tulips was probably first described in 1830 by Madame Libert, in connection with an herbarium specimen (Crypt. Ard. No. 36). She evidently observed only the sclerotia. She describes the fungus from the sclerotia as *Sclerotium Tulipae* Libert. From her description it is evident that she had studied the sclerotia of *Botrytis parasitica* Cavara (Saccardo, 1888-89).

The disease was first carefully observed by Cavara (1888), in upper Italy. However, Ritzema Bos (1903a:26) thinks Wakker (1885:22) had the same disease under consideration before Cavara's publication appeared. He called it "tulpenziekte." Ritzema Bos (1903a:25) states that the disease had been known in Holland for more than twenty years, but that he is not certain when it first became seriously destructive there. In 1890 affected tulip bulbs were sent to him from Norway. The work of Ritzema Bos, while in some respects not very accurate, was valuable in that it attracted attention to the importance of the disease. He began his studies in 1896 and published several papers on the subject.

Carruthers (1901:246) notes the occurrence of the disease in Northamptonshire and Cambridge, England, in 1901. It was reported near St. Petersburg in 1911 (Elenkin, 1911). Klebahn (1904:18) mentions its appearance in Hamburg, Germany, in 1902, and in other parts of Germany

later. He has done some of the most important work in clearing up the confusion in regard to the various sclerotial diseases of tulips and their life histories.

The appearance of the disease in America was first recorded by Halsted (1902). He had received in 1901, from a grower at Cape May, New Jersey, a diseased specimen, the bulb of which had originally been obtained from Holland. He stated that the disease had also occurred the previous season (1902:438). Obviously, therefore, it was introduced directly from Holland.

In a letter to Professor H. H. Whetzel, of Cornell University, Professor W. J. Morse, of the Maine Agricultural Experiment Station, mentions some unpublished records of the appearance of the disease at Barrington, Nova Scotia, in 1904, at Cobourg, Ontario, in 1906, and at Cartine, Maine, in 1910. There are also later notes. Professor Whetzel and the writer have received or collected specimens from Amsterdam, Sassenheim, and Aalsmeer, in Holland; from Germany; from Ithaca, McGraw, Garden City, Jamaica, and Brooklyn, in New York State; from Madison, Wisconsin; from Manistee, Michigan; from Washington, D. C.; from Bellingham, Washington; and from Carthage, Missouri. There is no doubt that the disease is widespread throughout the United States and Canada, and it probably will be found wherever tulips are grown.

ECONOMIC IMPORTANCE

There are apparently no exact figures available regarding the amount of damage from the Botrytis blight. Both Ritzema Bos and Klebahn speak of the great loss which this disease occasions to both field growers and florists. In fact, Ritzema Bos (1903:91) was engaged for a time by a growers' association to investigate the disease.

Elenkin (1911) reports that in 1911, near St. Petersburg, Russia, 50 per cent of the tulip crop was destroyed by this and other tulip diseases. A collection and observations made by Whetzel at the New York Botanical Garden in 1916 show the Botrytis blight to have been severe there at that time. Occurrence of the disease is recorded also by Stout (1918:241), and letters and specimens from Dr. David Griffiths indicate that it was very prevalent in the Federal Government's bulb gardens at Bellingham, Washington, in 1917.

In the spring of 1917 the writer observed the disease in an epiphytotic condition. Most of the tulip tops in the ornamental beds in the Cornell University campus were severely attacked. These were late, or Darwin, tulips, and counts made on one variety, Spathulata, showed 100 per cent of the leaves diseased, of which 33 per cent were strongly infected and 67 per cent only slightly. Of the stalks, 98 per cent were diseased, 23 per cent severely and 75 per cent slightly. The bulbs all showed slight infections, but it is uncertain whether these were infections by *Botrytis Tulipae* or by *Penicillium* sp. However, in the variety Spathulata 4.6 per cent of unmistakable Botrytis lesions were found, and in the variety Mrs. Grover Cleveland, 5.2 per cent. The presence of sclerotia in these lesions made identification certain. These were probably lesions from the previous year and they show how small an amount of original inoculum is necessary to produce a severe infection on the tulip tops. Accordingly it is impossible to lay too much emphasis on the selection of clean bulbs. The writer believes that this is the most important disease of the tulip in this country.

SYMPTOMS

On the bulbs

On the brown outer skin, or husk, of the affected bulbs, small black sclerotia may frequently be found, about 1 millimeter in diameter. They appear also on the old, dried, flower stalk of the previous season, which sometimes remains attached to the bulb (fig. 22). The removal of this papery, brown skin often reveals lesions on the outer, white, bulb scale which might otherwise have escaped notice. These lesions vary from deep yellow to brown, are usually circular in outline, and have a definite margin which may be somewhat raised. The central part is ordinarily depressed and may have on its surface small black sclerotia (fig. 23). The lesions are formed sometimes at the apex of the bulb, sometimes at the base, but more often in the region between. Less frequently the sclerotia may appear white, which is due to their immaturity. By removing the outer, fleshy scale and examining its inner side, it will be seen that some of the lesions have penetrated almost to the inner surface. They rarely extend into the scales beneath.

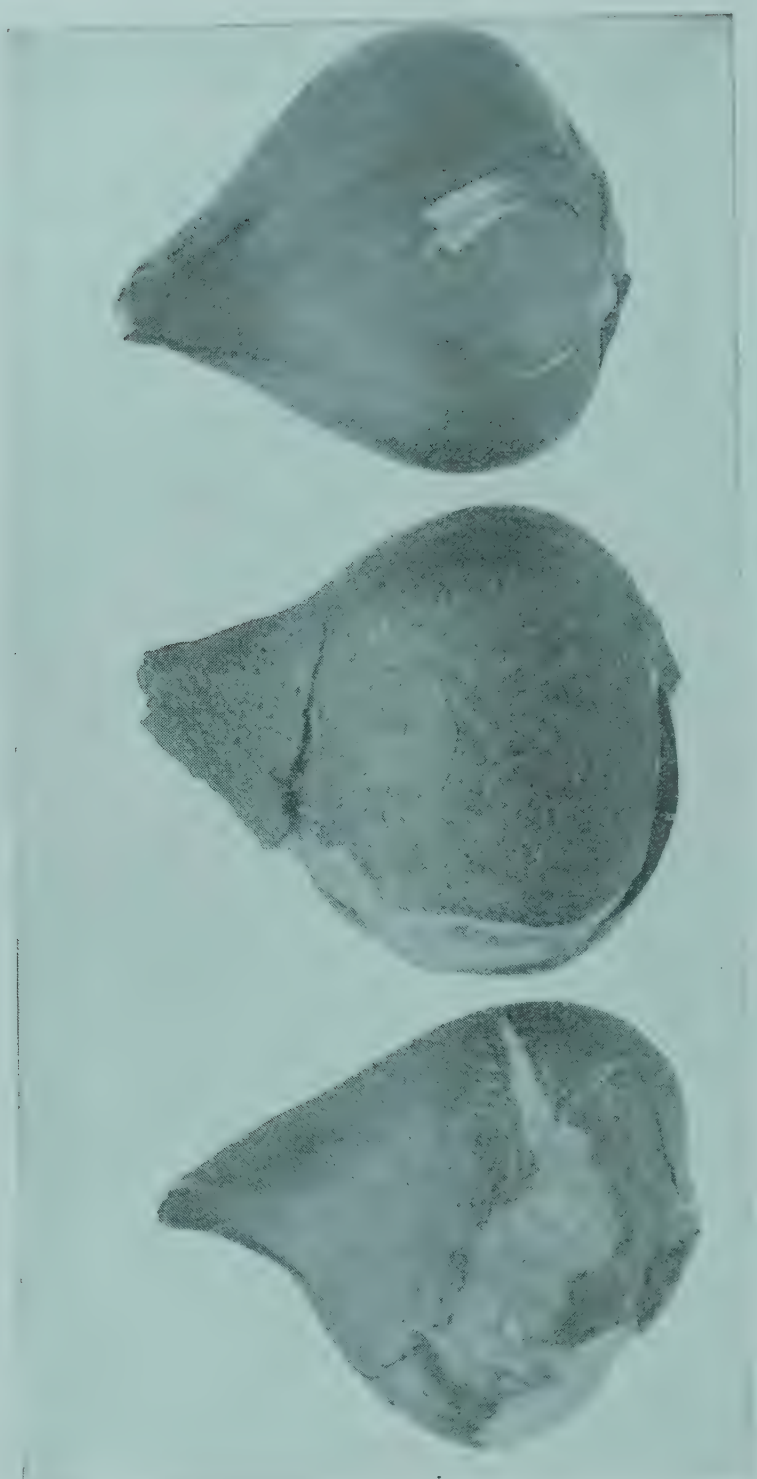

FIG. 22. SCLEROTIA OF BOTRYTIS TULIPAE

Showing them attached to the brown outer skin and the old, dried, flower stalk of dormant bulbs. Natural size

Under warm, humid conditions, a large part of the outer scale may become affected, and in some cases it is so densely covered with sclerotia that these coalesce and form a crust.

Care must be exercised not to confuse the lesions on the bulbs due to the very common Penicillium rot with those caused by *Botrytis Tulipae.*

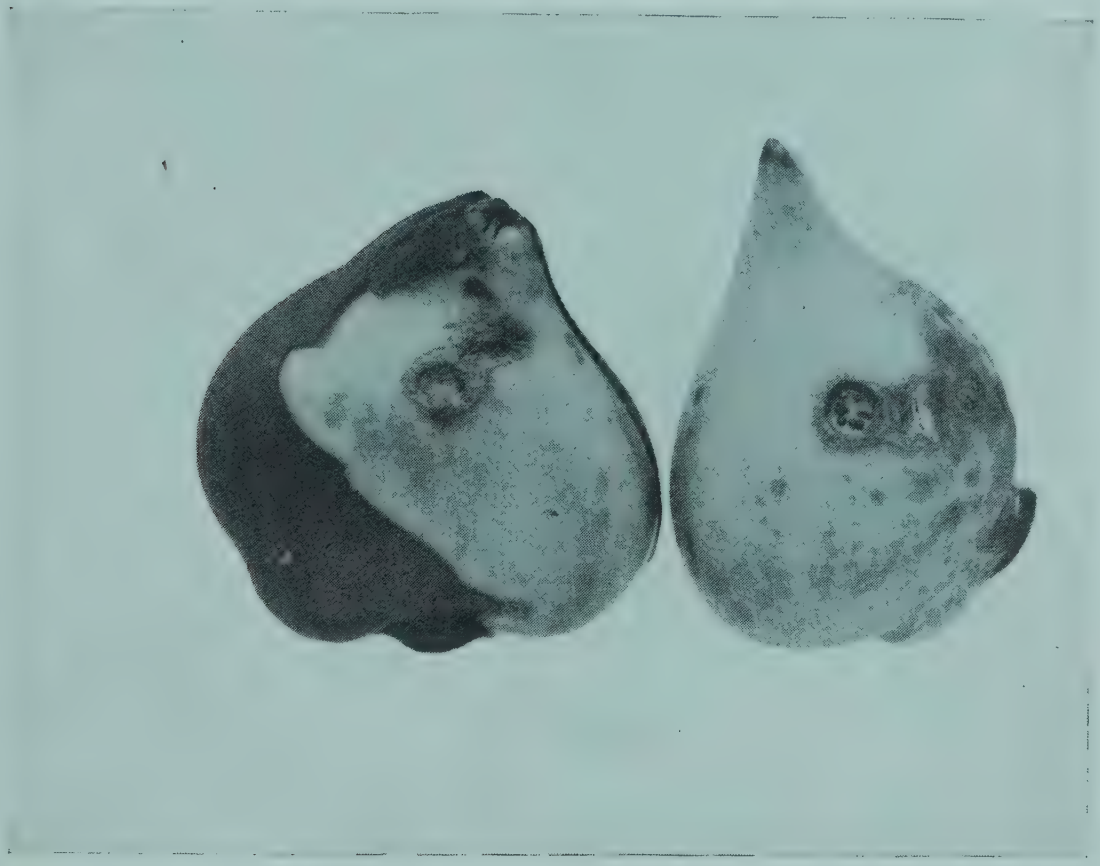

FIG. 23. BOTRYTIS BLIGHT LESIONS ON THE BULBS

The lesions in the outer, fleshy, bulb scale are depressed and show sclerotia on their surface. Natural size

This is especially true of the incipient lesions which, in these two diseases, are often found almost impossible to differentiate. In general, the lesions of the Penicillium rot are more indefinite in outline and of a lighter yellow color, are usually raised and uneven, and do not, of course, have sclerotia on their surface. The appearance of green mold, which forms under favorable conditions, is a distinguishing characteristic.

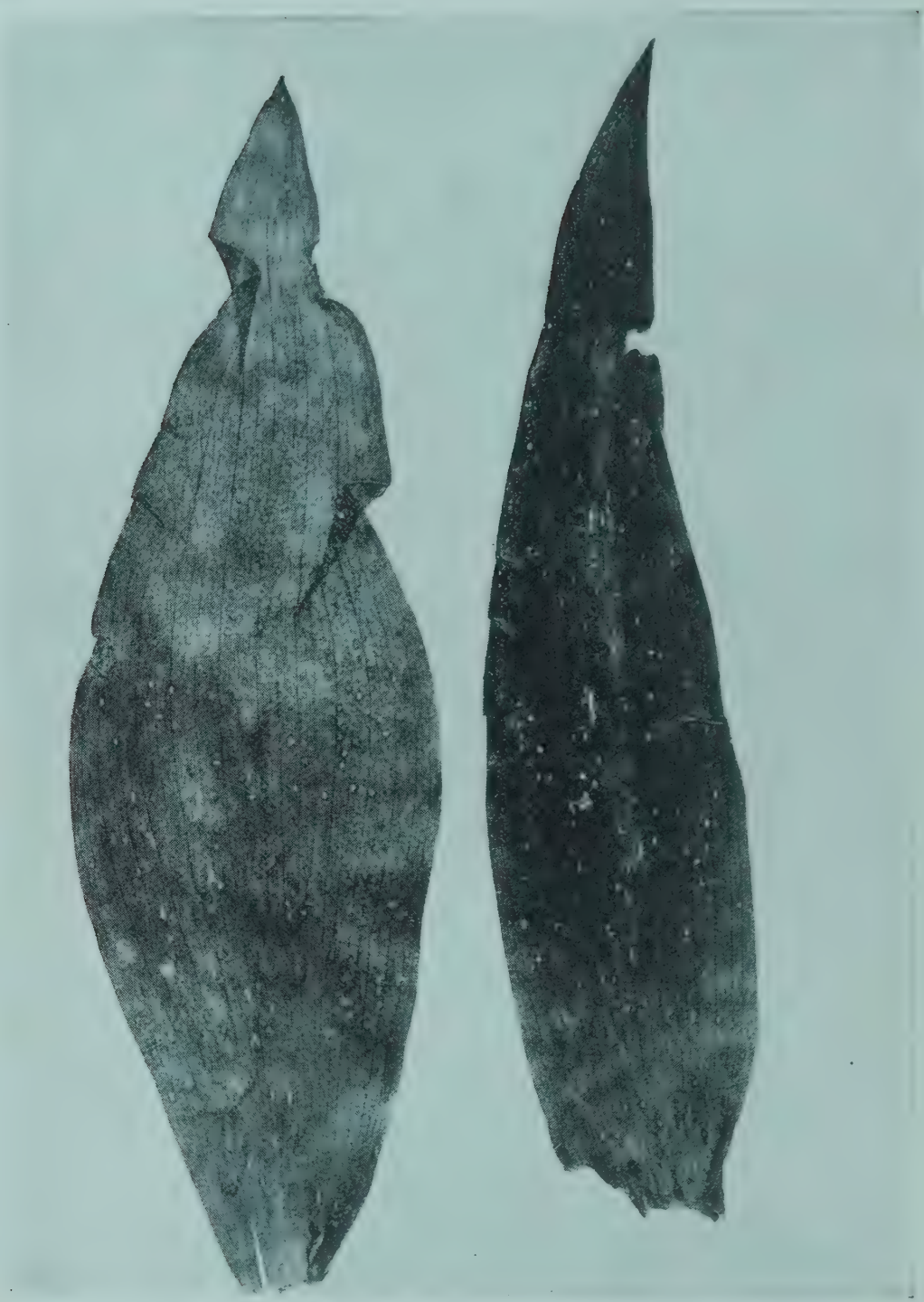

FIG. 24. BOTRYTIS BLIGHT LESIONS ON THE LEAVES
Young lesions. Three-fifths natural size

On the leaves

On the leaves the lesions show first as minute, yellowish spots, somewhat elongate in the direction of the leaf veins and surrounded by a darker,

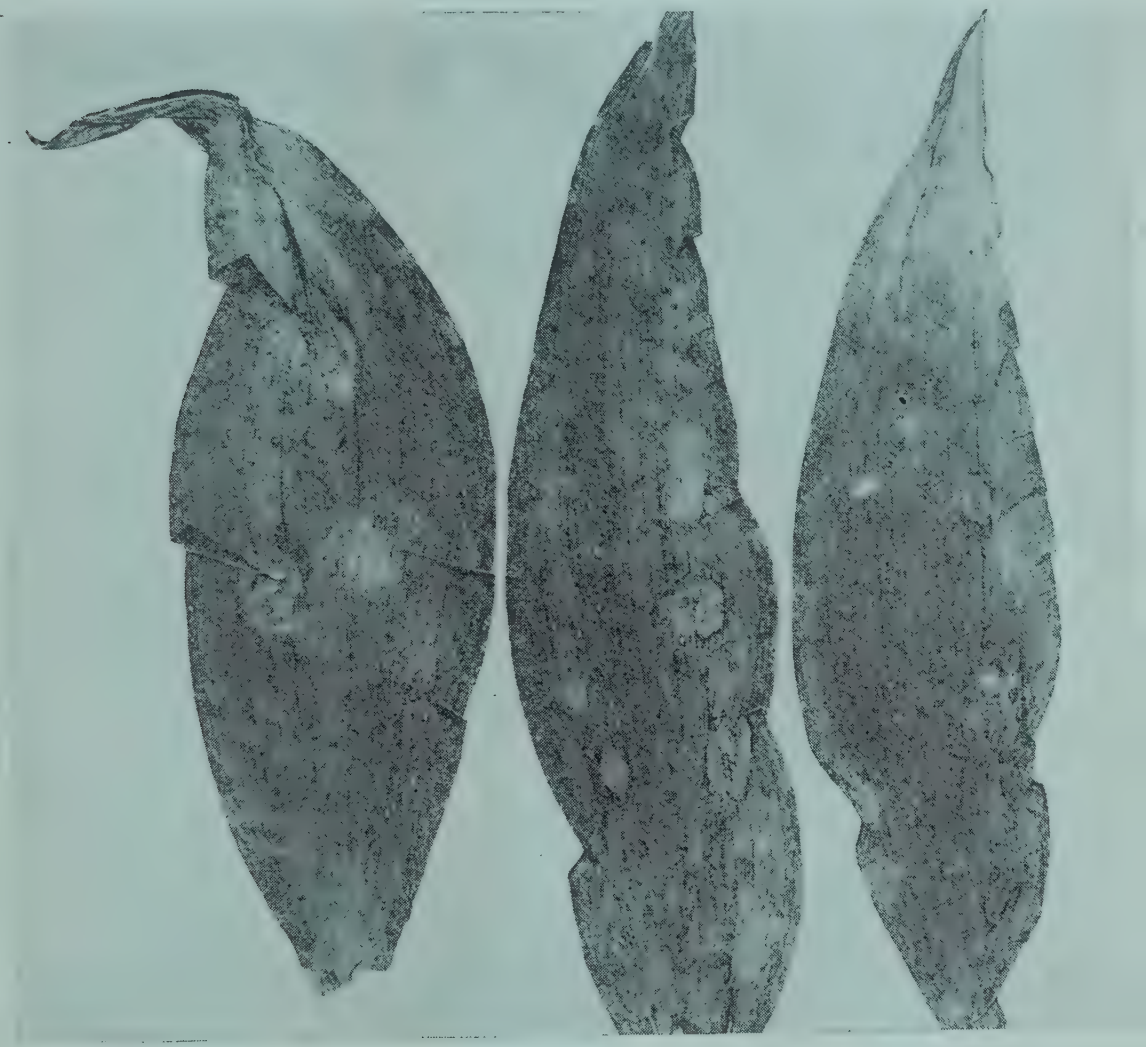

FIG. 25. BOTRYTIS BLIGHT LESIONS ON THE LEAVES
Lesions of a more advanced stage of development. One-half natural size

water-soaked area. They are slightly sunken and give the leaf a speckled appearance. As they enlarge, the areas become more depressed, the

FIG. 26. BOTRYTIS BLIGHT LESIONS ON THE LEAVES
Peculiar twisting of leaves due to a marginal lesion. Natural size

color changes to a whitish gray with a brownish tinge, and a translucent or water-soaked area appears about the margin. At this stage the margins of the lesions are quite definite (fig. 24). Toward the center abundant conidiophores are often produced. Under favorable conditions the lesions enlarge still farther, coalesce, and frequently involve the entire leaf. If a lesion develops toward the base of a leaf, it may cause the leaf to break over. When an infection takes place on the margin of the leaf near the tip, there results the characteristic appearance shown in figure 26. This wrinkling and bending of the leaf to one side is due to the more rapid growth of the healthy tissue opposite the lesion. (Klebahn, 1905:4).

Both young and old lesions are found on the same leaf showing that infections take place continuously (fig. 25). The outer sheathing leaf is likely to be attacked before the others, probably being infected as it emerges from the bulb. It bends downward and usually is abundantly covered with conidiophores (fig. 27).

FIG. 27. A DISEASED PLANT

Showing the outer sheathing leaf infected by contact with a lesion at the tip of the bulb. Note the abundance of conidiophores which give rise to inoculum for secondary infections. Natural size

On the flowers

The lesions on the flowers (Plate XXXIII) are very striking, especially on red varieties of tulips. They begin as minute spots, whitish to light brown, the color being bleached from the perianth. These spots are

FIG. 28. LESIONS ON THE FLOWER
Natural size

evenly distributed over the surface and usually show no Botrytis fructification (fig. 28). After the lesions enlarge, however, they turn a deeper brown and involve the entire segment of the perianth, which finally becomes dry and wrinkled. At this time they show abundant conidiophores. The whole flower may be affected and appear blighted.

FIG. 29. BUD BLIGHT SHOWING THE BLANCHING OF THE INFECTED TISSUE
Natural size

Indeed, this blighting may take place when the flower is still in the bud and prevent it from opening. Such a typical bud blight is reproduced in figure 29.

On the stalks

While the lesions on the stalks are still small, they have much the same appearance as those on the leaves except that they are more elongate and more depressed. They are of a light brownish color in the center, and are surrounded by a water-soaked area. Older lesions near the base of the stalk appear as dark brown patches and often bear sclerotia on their surfaces, while those higher on the stalk, usually originating in the leaf axils, are grayish white and are covered with conidiophores. Both this blanching effect and the conidial layer are well illustrated in figure 30.

The extension of the lesion through the stem causes the latter to weaken at the point of attack and break over. If the lesion is near the base, the whole plant topples over; if it is higher up, the flower droops.

ETIOLOGY

Nomenclature

The tulip disease under discussion is caused by *Botrytis Tulipae* (Libert) comb. nov. A sclerotial form, referred to the form genus Sclerotium by Madame Libert, in 1830, belongs to this species. She called it *Sclerotium Tulipae* and was the first to describe it (Crypt. Ard., no. 36). As previously mentioned, she apparently did not observe the conidial form. Her original description, which the writer has not been able to see, is taken from Klebahn (1907:5) who quotes it as follows:

Sclerotium Tulipae, N. Sparsum, adnatum, parvum, ovale, pallide fuscum, laeve, demum nigrum, rugosum, intus album. Ad caules, pericarpia et semina *Tulipae Gesnerianae*. Autumno.

In 1836 the species was again designated as *Sclerotium Tulipae* by Weinmann (1836:647). Sometime between 1841 and 1859 it was once more described in connection with an herbarium specimen, this time by Westendorp. He called it *Sclerotium entogenum* (Herb. crypt. Belg., no. 827). Finally Cavara (1888) described the fungus more completely,

FIG. 30. DISEASED STALKS
Natural size

including both the conidial and the sclerotial stages, which he assumed belonged to the same species. His description is as follows:

Botrytis parasitica nov. sp. Hyphis cinereis sparsis, erectis, articulo basali inflato; gonidiis ovatis, magnis, breviter pedicellatis, in ramulis minutis, capitatis, umbellatim dispositis; hyalinis vel dilute cinereis, 16–20 x 10–13 μ.

Forma scleroziale.

Sclerotium Tulipae Lib. Haemisphaericum, vel oblongum, nigrum, vix rugosum, superficiale vel immersum, intus albidum $\frac{1}{2}$–1 mm. latum.

Hab. Ad folia, caules, petala, et capsulas *Tulipae Gesnerianae* in Horto botanico ticinensi.

Cavara (1888:432) justifies his description of this species as a new one on the basis of morphological differences and also because of its strong parasitic action. In his discussion of nomenclature, he says that *Sclerotium Tulipae* Terry, which infects tulips in the south of France, according to Saccardo (1888–89,) is probably a synonym of *Sclerotium cepivorum* var. *Tulipae* Desm., and perhaps is the same as *Scl. cepae* Desm. Cavara was not able to compare specimens of *Scl. Tulipae* Terry with *Scl. Tulipae* Lib. The writer, however, had an opportunity to examine a specimen of the former at the herbarium of the New York Botanical Garden. This specimen consists of three or four sclerotia with no adhering plant material. The sclerotia are large, however, and are not those of *Botrytis Tulipae* (Lib.) comb. nov. At the same place the author was able to see some of the collection of Cavara designated *Botrytis parasitica* Cav., and found it to be identical with his own collections.

Massee (1899:383) describes the organism as *Sclerotinia parasitica*. This description was not based on a perfect stage and in Massee's key is placed under "Conodial form only known." Since there is no evidence that the species under consideration is a Sclerotinia, this name is not valid. Massee's description is as follows:

Sclerotinia parasitica, Massee; *Botrytis parasitica*, Cavara. Conidiophores grey, scattered, erect, basal joint inflated; conidia obovate, large, shortly pedicellate, on short umbellately arranged branchlets, hyaline or tinged grey, 16–21 x 10–13 μ; sclerotia formed in the parenchyma of the host, globose-depressed, smooth, greyish, then black, 2–3 mm. diam., sometimes numerous, and forming black crusts.

Botrytis on leaves, stem, and flowers of cultivated tulips; sclerotia more especially on the bulbs.

Distr. Holland, Britain.

A consideration of these facts has led to the following designation of the species:

Botrytis Tulipae (Libert) comb. nov.

Sclerotium Tulipae Lib. Crypt. Ard., no. 36. 1830.
Sclerotium Tulipae Weinn. Hym. Ross., p. 647. 1836.
Sclerotium entogenum West. Herb. crypt. Belg., no. 827. 1841–1859.
Botrytis parasitica Cav. Appunti die Pathologia Vegetale. Ist. Bot. R. Univ. Pavia. Atti 2:1:432. 1888.
Sclerotinia parasitica Massee. A text book of plant diseases, p. 383. 1899.

Botrytis Tulipae (Libert) comb. nov. may be briefly described as follows: Mycelium variable in diameter, often anastomosing, branches not constricted at the base; conidiophores arising directly from the mycelium, erect, brown in color, proliferating, twisting on their axils when dry, slightly swollen at the base; branches of conidiophore arising at an angle of about 60 degrees, dichotomous, not streptiform, apices swollen; conidia large, 12-24 x 10-20 μ, obovate, reddish brown in mass; microscopically gray to hyaline, smooth with a short stalk, often or commonly not remaining attached; sclerotia at first white, finally black, small, 1-2 millimeters in diameter, circular or somewhat elliptical in outline, flattened vertically and often convex. Microconidia globose, about 3 μ in diameter, occurring on special penicillate, obclavate conidiophores arising in white tufts from the substratum (fig. 40). Parasitic on *Tulipa* spp.

Cavara (1888:432) says that *Sclerotium entogenum* West. develops on the stalks of asparagus and does not differ greatly from *Scl. Tulipae* Lib.; he says, moreover, that Westendorp thinks *Sclerotium entogenum* West. should be regarded as the type of the species. *Sclerotium Tuliparum* Klebahn is a species which must not be confused with *Botrytis Tulipae.* It is a large, sclerotial form with which no conidial stage has yet been connected.

The species must, therefore, still be classified among the Hyphomycetes of the Fungi Imperfecti. It is placed there by Lindau (1900:435) in the subgroup Mucedinaceae-Hyalosporae-Botrytideae.

Klebahn (1904:21), from his studies on *B. Tulipae*, seems certain of the connection of the sclerotia occurring on the tulip bulbs with the conidial form on the leaves. However, as he did not use pure-culture methods, it seemed desirable to clear up this point. Pure cultures were made by the writer from the sclerotia occurring on the bulb and from conidia on the leaves of the same tulip plant. These cultures were identical, and when inoculated into sterilized tulip leaves both produced normal conidia and sclerotia. Both also caused infection of healthy tulip plants.

Morphology

The mycelium shows no peculiar characteristics. It varies in diameter, depending on the conditions under which it lives. The branches are not constricted where they join the parent hypha. Anastomosing is frequent (fig. 31). The conidiophores, when mature, are deep brown in color except near the base, where they are hyaline. They are indeterminate in length, for under favorable conditions, after forming one head of conidia terminally, the main axis may proliferate and form another head (fig. 50). This may be repeated until finally there are several clusters of conidia on a single conidiophore (fig. 32). It should be remembered that although some of these clusters appear to be lateral, they are really formed terminally. When

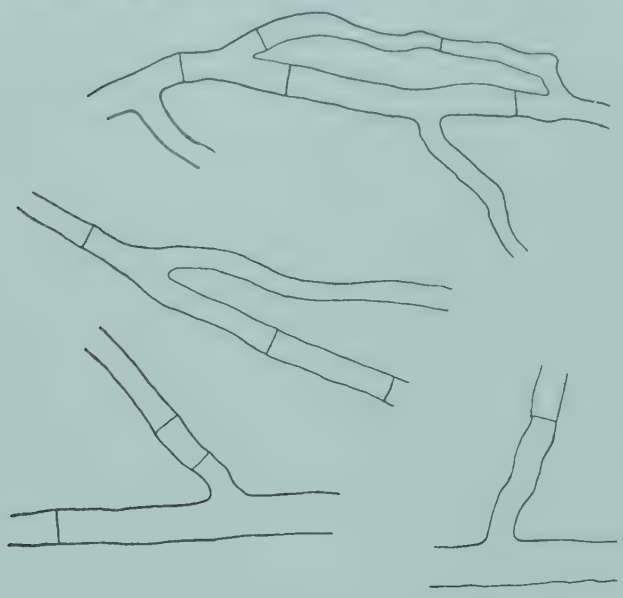

FIG. 31. MYCELIUM OF BOTRYTIS TULIPAE. × 600
Type of branching and anastomosing of the hyphae. (Camera-lucida drawing)

FIG. 32. CONIDIOPHORE OF BOTRYTIS TULIPAE. × 67
A conidiophore unmounted. The several clusters of conidia due to proliferation, and the twisting of the stalk when dry, are both visible. (Camera-lucida drawing)

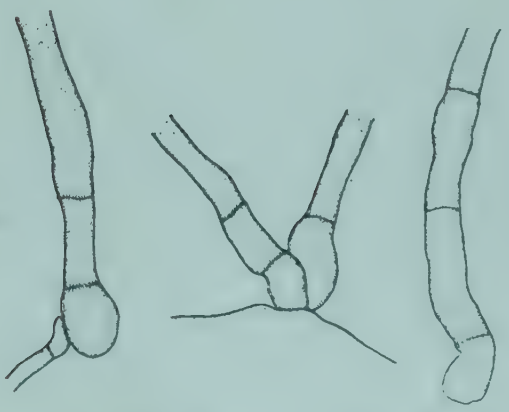

FIG. 33. SWOLLEN BASES OF CONIDIOPHORES OF BOTRYTIS TULIPAE. × 600
(Camera-lucida drawing)

dry, the conidiophore is flattened and twisted on its axis, and is slightly swollen at the base (fig. 33).

The branches of the conidiophore rise from the main stalk at an angle of about 60 degrees, and their ultimate ends, which bear the conidia, are somewhat swollen. The conidia are produced on these swollen ends by a pushing out of the protoplasm in a bud-like manner, but they shortly assume a definite shape. When mature, they remain attached by short sterigmata (figs. 34 and 35). Various stages of conidial formation

FIG. 34. ATTACHMENT OF CONIDIA OF BOTRYTIS TULIPAE. × 600

Camera-lucida outline of conidia shown in fig. 35. Proliferation of the conidiophore has taken place after the formation of conidia on the head.

FIG. 35. ATTACHMENT OF CONIDIA OF BOTRYTIS TULIPAE. × 840

Note the short sterigma. These conidia are mature. (Photomicrograph)

are shown in figures 36 and 37.[3] Usually young conidiophores were chosen for study because of the firmer attachment of the conidia. The preparation of the mounts required considerable patience because of the delicate attachment of the conidia, and oftentimes many mounts were prepared before one was obtained which showed clearly the details of structure. When young, the conidia are hyaline, but as they mature they assume, in mass, a brownish color. Microscopical examination shows that most of this color is in the spore wall. The conidia are obovate, and when shed, the short sterigmata may sometimes be seen still attached to the spores.

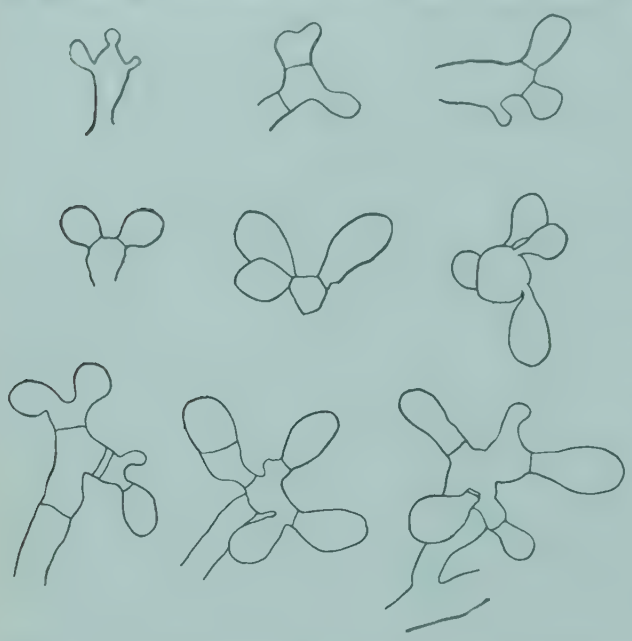

FIG. 36. DEVELOPMENT OF CONIDIA OF BOTRYTIS TULIPAE. × 600

Illustrating the bud-like manner of their formation. (Camera-lucida drawing)

The conidia vary considerably in length and to a less extent in width, but this variation does not depart greatly from a mean which is more or less constant. This is shown graphically in figure 38, which represents the measurements of one hundred spores. One curve expresses the variation of the spore length and the other that of the spore width.

The spores measured were from single-spore cultures and developed on sterilized tulip leaves in petri dishes. Abundant conidial fructifications were formed which were practically identical in appearance with those occurring in nature. They were mounted in the mounting fluid previously described[3] and were measured under the oil-immersion lens by

[3] In studying the detail of the conidiophore, especially the attachment of the conidia, satisfactory mounts were obtained by first adding to the material on the slide a drop of 70-per-cent alcohol in order to "wet" the conidiophores rapidly. The material was then flooded immediately with a mounting fluid prepared by mixing equal parts of 2-per-cent potassium acetate in water and 40-per-cent glycerin in alcohol and then adding a trace of copper acetate. The excess mounting fluid was removed with filter paper and the mount covered with a cover glass. Such mounts keep very well, do not dry out, and may be kept permanently when ringed with balsam or gold size.

means of camera-lucida drawings. One hundred spores were outlined and the outlines measured with a millimeter rule. The error in measuring was calculated to be less than 2 per cent. On the basis of these measurements the average limits of variation may be placed at 12-24 x 10-20 μ.

These figures do not show the distribution of the spores within these limits. From figure 38, however, it is apparent that the greater number have a length of 16-17 μ and a width of 9-10 μ. These measurements were checked with those of spores from another culture derived from a different locality. Measurements made of the spores of a large number of Botrytis specimens seem to show that one hundred conidia suffice to establish the mode for a given species.

FIG. 37. DEVELOPMENT OF CONIDIA OF BOTRYTIS TULIPAE. × 600

Mature conidia. (Camera-lucida drawing)

The sclerotia as formed in a petri-dish culture, (fig. 39) are at first white, and later, a shiny black. They are circular, elliptical, or somewhat irregular in outline, flattened vertically, and often slightly convex. They might be described by the term "loaf-shaped." Ordinarily the sclerotia are about one millimeter in diameter. Their size may be considerably affected by the amount of drying to which they are subjected.

Physiology

Growth

Botrytis Tulipae grows very readily on the various kinds of media, both liquid and solid, on which it has been planted. In the writer's experimental work the commonest medium employed was potato-dextrose agar. On this the fungus makes a rapid, fluffy mycelial growth, which later becomes appressed to the surface of the agar and the sclerotia then begin to form. These are very numerous and are imbedded in a tough, mycelial membrane which covers the surface of the substratum. As mentioned under *Conidia production*, conidia are rarely formed in such cultures. Moreover, there is scarcely any color production in this medium.

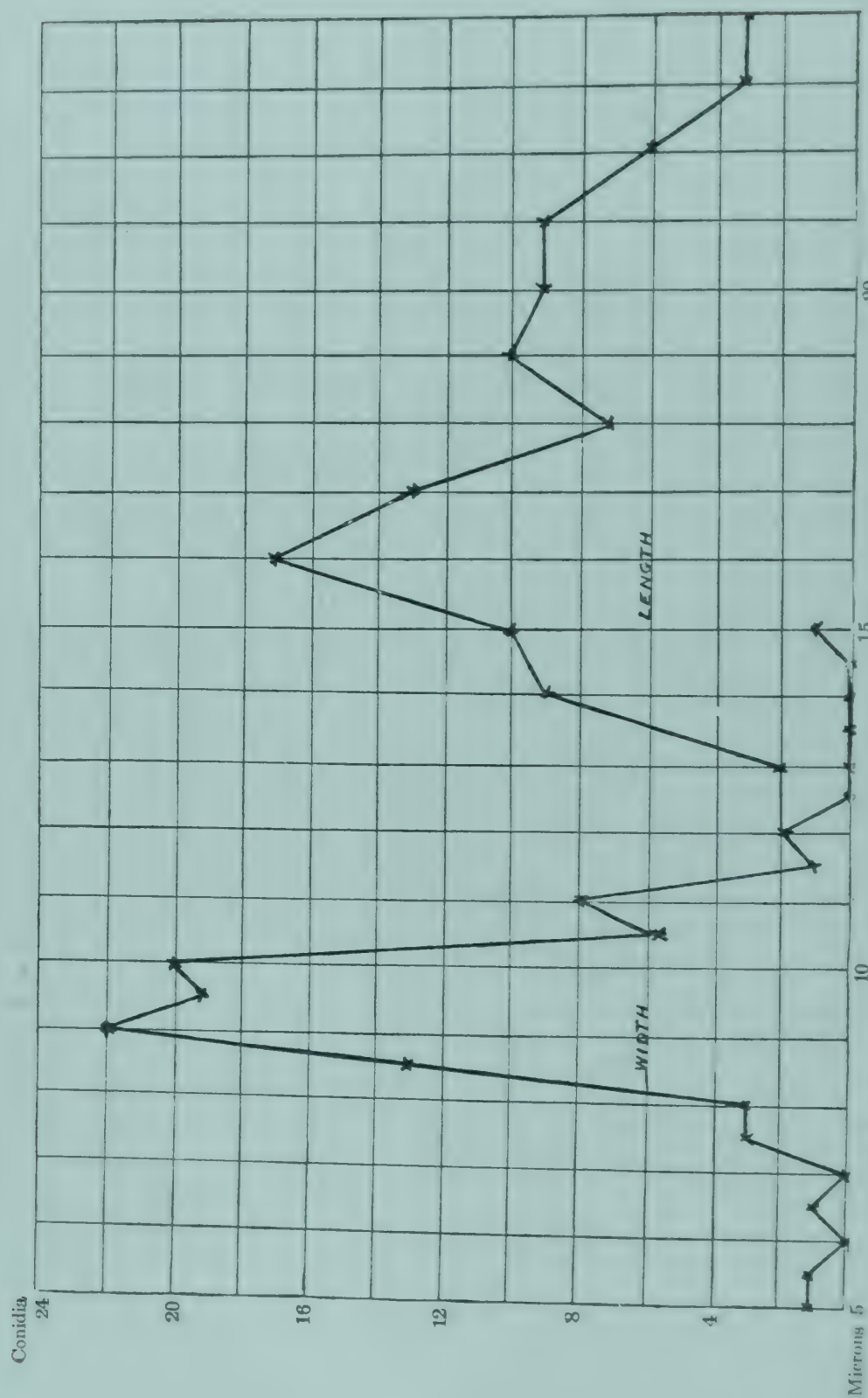

FIG. 38. GRAPHIC REPRESENTATION OF CONIDIAL MEASUREMENTS OF BOTRYTIS TULIPAE

Showing the distribution of 100 conidia. The ordinates show the number of conidia; the abcissae, their length or width in microns

It is of little importance to describe at length the growth on other media: sucrose is utilized as a source of carbon apparently as successfully as glucose; on a glucose solution, without mineral nutrition, the growth is very poor; on plain agar and water the growth is sparse and the mycelium tends to spread; but on agar containing a mineral-nutrient solution, with

FIG. 39. SCLEROTIA OF BOTRYTIS TULIPAE

As formed in a petri-dish culture on potato agar. Natural size

no source of carbon, an excellent growth takes place, even better, perhaps, than that on potato-dextrose agar. This indicates that the carbohydrates of the agar itself are being utilized. With oxalic acid as a carbon source, the growth is poor.

Growth is best on an acid medium, and, although no experiments have been made to determine the range of acidity, good development has

always been observed when the acidity was approximately +20 according to Fuller's scale. Perhaps the range is as wide as that determined by Munn (1917:407-408) for the growth of *Botrytis Allii*.

Conidia production

Although conidia are produced abundantly in nature on tulip leaves, in agar culture under the ordinary laboratory conditions they rarely appear. The fungus tends rather to form sclerotia. However, early in 1917 the writer observed for the first time that conidia had formed under these conditions when some conidiophores developed in five petri-dish cultures. It should be noted that these conidia were produced without any special treatment, and that, although they were produced once or twice afterward, this is rather unusual under the conditions obtaining in ordinary culture vessels.

On March 17, 1917, sterilized tulip leaves in large test tubes, 20 x 2.5 centimeters in size were inoculated with cultures of three different strains in duplicate. In two of these strains a fluffy mycelium soon developed, which spread along the leaves. After about ten days conidiophores began to develop, usually toward the top of the culture, and by March 31 there was an abundant development of conidiophores close to the surface of the leaves just beyond the aerial mycelium as well as on the mycelium itself. The conidia produced were able to cause infection in healthy tulips. This experiment was repeated on April 27, 1917, and the cultures were observed daily in order to note the first appearance of the conidia. This occurred in five cultures on May 8.

Some time later, Professor Whetzel suggested that a partial drying of the plate cultures, after a good growth of mycelium had started, might produce conidia. This experiment was accordingly performed, and the partial drying was accomplished by so placing the petri-dish cover as to expose part of the agar surface, thus permitting more rapid evaporation. The petri dishes were usually left overnight in a dust-free chamber and were tightly covered again the next morning. Conidia were in this way produced successfully in a large number of instances, not only from *B. Tulipae*, but also from other Botrytis species which do not readily fruit in culture. On halves of sterilized tulip bulbs in petri dishes the fungus was also found to fruit abundantly. There seems to be a relation between conidial

production and the relative humidity over the culture, or, to state it more concisely, a relation between the rate of evaporation and conidial production.

There is, perhaps, something inherent in the nature of the host tissue which makes it an especially good substratum for the production of conidia; but it is more likely that the fungus finds in such cultures more variation in the moisture relations. This would explain why, in the experiments with sterilized tulip leaves, the conidia were not produced uniformly throughout the culture but only on a limited area toward the top of the culture tube, where the moisture relations were presumably most favorable.

Dissemination of conidia

The peculiar twisting of the conidiophores, already mentioned, is thought to have some relation to the dissemination of the conidia. In the first place, the conidia fall away very readily. This becomes obvious when an attempt is made to mount conidiophores bearing conidia in a liquid medium or if a conidiophore is jarred slightly. Secondly, the conidiophores are very hygroscopic, and a small change in the atmospheric moisture will cause them to twist with considerable violence and frequently even to dislodge the conidia. This phenomenon can be easily observed in this and in other Botrytis species by placing the specimen under a binocular microscope. Merely breathing on it gently suffices to produce these contortions. It may be concluded that in nature, owing to the frequent changes in humidity that occur, conidia are commonly dislodged in this manner and carried off by air currents.

The conidia are usually wind-borne. The writer has found that inoculations with conidia are best made by either blowing or dusting them on the host plants and subsequently spraying water on them with an atomizer.

Pathogenicity

The pathogenicity of *Botrytis Tulipae* was first demonstrated by Klebahn (1905:6), who inoculated tulip bulbs with sclerotia from a pure culture. However, he appears not to have done much exact inoculation work, and, with the exception of the experiment cited, did not use pure cultures in his infection tests. The writer does not consider that Ritzema Bos

(1903a:24) demonstrated the pathogenicity of the organism by his investigations, for he did not use pure-culture methods, but merely developed Botrytis conidia on leaves in moist chambers and then dusted the conidia on sliced bulbs, causing the bulbs thus treated to decay.

Experimental methods

The writer made isolations of the fungus from material obtained from many localities in Holland, Germany, England, Canada, and the United States. These isolations were made both from dry specimens (for it was found that the fungus would retain its vitality for a long time without moisture) and from recently infected plants. Moreover, they were made from sclerotia, mycelium, and conidia from various parts of the host — bulbs, stalks, leaves, buds, perianth, and stamens.

Although Klebahn (1905:12) found it difficult to obtain pure cultures from the sclerotia, the writer has experienced little difficulty in isolating from sclerotia by the following method: The sclerotium is rubbed free from all adhering material with a clean piece of cheesecloth, and is dipped for instant in 95-per-cent alcohol to remove the surface film of air, that is, to wet the surface. It is then placed in a 1:1000 mercuric-chloride solution for about thirty seconds, after which it is quickly removed with sterilized forceps and placed in a drop of sterilized water in a sterilized petri dish. To thoroughly remove the mercuric chloride, the sclerotium is then rinsed in several successive drops of sterilized water in the same petri dish. Usually six washings are sufficient. The sclerotium, thus prepared, is cut into four pieces and planted on a poured plate of potato-dextrose agar. The whole operation should not take more than five minutes. The writer has used this method in isolating several hundred Botrytis specimens as well as specimens of other fungi, and rarely has a contamination occurred.

Fungi may be isolated from leaf tissue in this way if care is taken not to leave the material too long in the alcohol. In these experiments the mycelium was usually isolated from the leaf tissue and the stems by cleaning the epidermis with alcohol and then peeling it back, or often, when using stems and bulbs, by breaking or splitting them open so as to expose an uncontaminated surface. Small parts of the diseased tissue were then picked out with a sterilized, sharp-pointed scalpel and planted in agar.

Conidia were isolated in several ways. Sometimes they were blown over the surface of the agar from the bent end of a platinum needle. The needle was attached to a piece of glass tubing which served as a blowpipe. The tendency at first was to gather too many spores on the needle, but with practice a sparse sowing was readily made and transfers were then obtained from the resulting colonies. Another method was to pick off, with sharp-pointed forceps, a single conidiophore, under a binocular microscope if possible, and then touch it to an agar plate in several places. Pure cultures usually resulted from some of these plantings, and often all the cultures were pure.

Pure line cultures were obtained in two ways: first, by planting the fungus on a poured plate of plain agar and water, which caused the mycelium to spread out in its growth so that a single mycelial tip could be marked under the low power, cut off, and transferred; secondly, by the isolation of a single spore. In the latter method, which was the one most frequently employed, care was necessary lest more than a single spore should be obtained. A thin layer of agar containing a few conidia was poured into a petri dish and the spores were allowed to germinate slightly. After a conidium was marked and transferred to a poured plate, a microscopical examination was always made to ascertain positively that not more than one spore had been cut out. The growth of these cultures on potato agar is characteristic and is described under *Physiology* (page 355).

Both mycelium and conidia were used as inoculum. The mycelium inoculum was prepared by growing the fungus in a petri-dish culture until the colony had reached the size of an inch or so in diameter. Small cubes of agar containing mycelium were then cut with a sterile scalpel from the edge of the colony and placed on the plant part to be inoculated, with the side containing the mycelium against the host. To prevent the inoculum from drying out, the plants were either placed in a large, moist chamber or covered with a bell glass or a lamp chimney. When it was desired to injure the inoculated parts, this was done by pricking a sterile, sharp-pointed scalpel through the agar block into the host tissue.

In using conidia, difficulty was at first experienced in attempting to spray the plants with spore suspensions in water. No infections resulted. As already mentioned, this is explained by the fact that the conidia are

not readily wet with water and consequently the water sprayed contained but few conidia in suspension. This was demonstrated by a microscopical examination of the drops on a slide sprayed with the suspension. Very few spores were found, and hence the chances for infection were slight. Since this method was unsatisfactory, an attempt was made to secure infection by dusting the conidia on with a camel's-hair brush. This proved to be very successful, and abundant infection resulted, both on dormant bulbs and on growing tulip plants. Plants inoculated in this manner were sprayed with sterile water from an atomizer and kept moist overnight.

Results of inoculations

The results obtained from inoculating dormant tulip bulbs with mycelium are shown in table 1. From this table it is clear that the dormant bulbs must be injured at the point of inoculation in order that

TABLE 1. RESULTS FROM INOCULATING DORMANT TULIP BULBS WITH MYCELIUM

Culture	Number of bulbs inoculated		Number of bulbs infected	
	Injured	Uninjured	Injured	Uninjured
B. 298	4	2	4	0
B. 163	2	1	2	0
B. 112	2	1	2	0
B. 149	2	1	2	0
B. XVII	2	1	2	0
B. XXVII	2	1	2	0
B. XXXII	2	1	2	0
Total	16	8	16	0

* The arabic numerals represent cultures from domestic sources, and the roman numerals, those of foreign origin.

mycelium may infect them. Briefly stated, the entire sixteen of the dormant bulbs which had been injured were infected by the inoculation, whereas none of the eight uninjured bulbs were thus affected. On the other hand, when ten bulbs were inoculated just after the flowers had been cut, all became infected, although only five were previously injured.

A summary of the results obtained from inoculating tulip stems with mycelium appears in table 2. From this table it is evident that the tulip stems inoculated with twelve different cultures of *Botrytis Tulipae*, five

TABLE 2. RESULTS FROM INOCULATING TULIP STEMS WITH MYCELIUM

Culture*	Number of stems inoculated		Number of stems infected	
	Injured	Uninjured	Injured	Uninjured
B. 298	3	3	3	3
B. XXVII	4	5	4	3
B. XXV	4	5	2	2
B. XXVI	4	5	4	5
B. XVII	4	5	4	5
B. XXXII	4	5	4	5
B. 112	3	3	3	2
B. 143	3	3	3	3
B. 149	3	3	3	3
B. 150	3	3	3	3
B. 163	4	5	4	5
B. 414	1	2	1	1
Total	40	47	38	40

* The arabic numerals represent cultures from domestic sources, and the roman numerals, those of foreign origin.

TABLE 3. RESULTS FROM INOCULATING TULIP LEAVES WITH MYCELIUM

Culture*	Number of leaves inoculated		Number of leaves infected	
	Injured	Uninjured	Injured	Uninjured
B. XXVII	1	2	1	0
B. XXV	1	2	1	2
B. XXVI	1	2	1	2
B. XVII	1	2	1	2
B. XXXII	1	2	1	2
B. 163	1	2	1	2
B. 414	1	2	1	1
Total	7	14	7	11

* The arabic numerals represent cultures from domestic sources, and the roman numerals, those of foreign origin.

from foreign sources and seven from domestic, showed thirty-eight infections out of forty when pricked with a needle after inoculation, and forty out of forty-seven when not injured in this way.

A summary of the results obtained from inoculating tulip leaves with mycelium is given in table 3. All seven leaves showed infections when inoculated and injured; of the uninjured leaves, eleven out of fourteen showed infections.

Tulip flowers were inoculated with mycelium, with results as given in table 4. The tulip flowers, like the leaves, were all seven infected when an injury was made at the point of inoculation. Out of fourteen not so injured after inoculation, twelve showed infections.

TABLE 4. RESULTS FROM INOCULATING TULIP FLOWERS WITH MYCELIUM

Culture*	Number of flowers inoculated		Number of flowers infected	
	Injured	Uninjured	Injured	Uninjured
B. XXVII	1	2	1	1
B. XXV	1	2	1	2
B. XXVI	1	2	1	2
B. XVII	1	2	1	2
B. XXXII	1	2	1	2
B. 163	1	2	1	2
B. 414	1	2	1	1
Total	7	14	7	12

* The arabic numerals represent cultures from domestic sources, and the roman numerals, those of foreign origin.

It should not be deduced that the lower proportion of infections in the uninjured leaves, stems, and flowers was owing to the inability of the fungus to penetrate uninjured tissue. The writer attributes it rather to experimental error; for the inoculum was more likely to be lost or dried out before infection had opportunity to take place than when it was placed at once in such intimate contact with the host tissue as was the case when the latter was injured.

On April 3, 1917, six dormant bulbs were dusted with conidia from a pure culture of strain B. XXVII, and by April 25 five of these were

strongly infected and some showed aerial mycelium arising from the lesions. On April 18, 1917, ten, clean, dormant bulbs were inoculated in the same manner with conidia from a culture of strain B. XXVII. In several days, nine of these showed numerous spots or streaks, varying in color from yellow to brown, where the conidia had been sown.

On March 30, 1917, at 5 p. m., four tulip leaves were dusted with conidia from a pure culture and the following morning at nine o'clock small water-soaked spots had appeared, a microscopical examination of the epidermis of which showed that the conidia had germinated and had penetrated the cuticle. On April 2 these spots showed a rusty color and were surrounded by translucent, water-soaked areas.

On April 1, 1917, at 4 p. m., three tulip plants in pots were inoculated with conidia of strain B. XXVII and placed under a large bell glass. On April 2, at 9 p. m., all had developed a considerable number of infections, as shown by the large number of small, yellow spots. These spots later become larger and of a somewhat reddish cast. About five days later the plants were severely diseased and showed a mycelial growth on the leaf surface. About seven days thereafter conidia were formed. On April 12 some sclerotia were noted in the leaf tissue.

On April 13, 1917, eight tulip plants were inoculated with conidia of strain B. XXVII and placed in a large moist chamber. On April 16 all showed numerous yellow-to-reddish spots on the leaves. A few similar spots appeared on the stems. By April 18, the small spots had coalesced and appeared as large, reddish lesions, some of which were covered with abundant conidiophores.

The inoculations with conidia are summarized in table 5. The plants were not mechanically injured at the time of inoculation.

TABLE 5. RESULTS FROM INOCULATING UNINJURED TULIP PLANTS WITH CONIDIA

Experiment	Culture	Plant part	Number inoculated	Number infected
16	B. XXVII	Bulb (dormant)	6	5
18	B. XXVII	Bulb (dormant)	10	9
14	B. XXVII	Leaves (detached)	4	4
15	B. XXVII	Tops	3	3
17	B. XXVII	Tops	8	8

In using mycelium as inoculum on the leaves and the stems, the lesions, after a short time, become as typical as those of the same age produced in nature. In the beginning, however, although they show the characteristic yellowing, they are not exactly like natural lesions, for they assume the shape of the agar block used in the inoculation. As the infection spreads, the region about the inoculum becomes water-soaked, then depressed, and finally dried out. At the last stage, the lesion assumes a dull gray color and produces fluffy mycelium and sometimes also a conidial layer. The lesions tend to elongate in the direction of the stem and the leaf. If an inoculation is made on the edge of a young leaf near the tip, the peculiar twisting described on page 323, under the heading *Symptoms*, results. The whole plant top may be involved as a result of such an inoculation (fig. 42). On the dormant bulbs, also, the lesions are typical (fig. 41) with a dark brown, shiny surface. In using conidia as inoculum, the lesions are typical from the start and are essentially as described on pages 319 to 328.

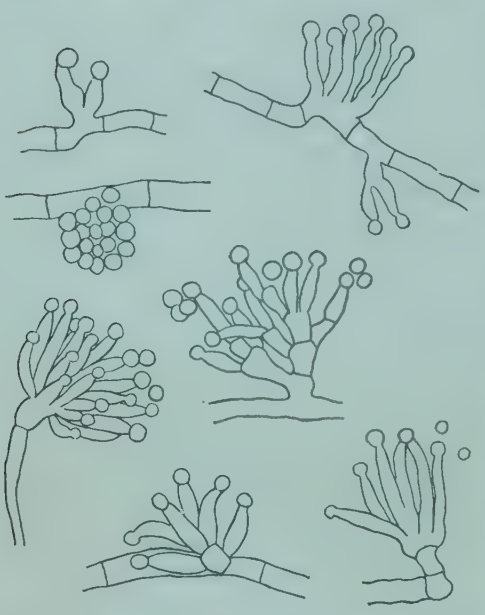

FIG. 40. MICROCONIDIA OF BOTRYTIS TULIPAE. × 600

(Camera-lucida drawing)

With but few exceptions, when infection was positive, the fungus in these experiments was re-isolated in pure culture by one of the isolation processes described under *Methods*, and checked identically with the original culture. Usually the tissue-planting method was the one employed.

In order to determine the range of parasitism of this species, a considerable number of experiments were made on both closely related and distantly related plants to find out whether *Botrytis Tulipae* is able to infect them.

The general results of these experiments appear in table 6. Certain of these, however, should be discussed more fully.

TABLE 6. RESULTS OF INOCULATION ON VARIOUS HOSTS FROM INOCULATING PLANTS NEARLY AND DISTANTLY RELATED TO THE TULIP

Plant	Inoculum	Number inoculated		Number infected	
		Injured	Uninjured	Injured	Uninjured
Lily of the valley	Mycelium	14	0	0	.....
Onion (leaves)	Mycelium	3	3	3	0
Onion (bulbs)	Mycelium	16	1	0	0
Onion (stems)	Mycelium	2	0	0	.....
Lilium sp.	Mycelium	6	6	0	0
Narcissus (leaves)	Mycelium	11	11	11	0
Narcissus (leaves)	Conidia	0	5	.....	0
Narcissus (stems)	Mycelium	3	3	3	0
Hyacinth (leaves)	Conidia	0	5	.....	0
Crocus (tops)	Mycelium	7	7	7	0
Crocus (bulbs)	Mycelium	5	5	5	1
Gladiolus	Mycelium	10	0	0	.....
Peony	Mycelium	19	0	3	.....
Potato	Mycelium	21	0	0	.....
Golden seal	Mycelium	6	0	0	.....

From table 6, the relation of *B. Tulipae* to certain plants is evident: it is not able to attack at all the lily of the valley, the lily, the gladiolus, the potato, or the goldenseal, and, probably, not the peony. However, this relation will be made clearer by a discussion of certain observations made during the attempts to cause infection on these plants.

Inoculation of onion.— Leaves and stalks of onion plants were inoculated with three different cultures, one of these a typical culture of *B. Tulipae.* In those plants that were injured at the time of inoculation, strong infection took place on the leaves but none occurred on the stems. On the uninjured plants there was no infection. To serve as checks, other plants were inoculated at the same time with

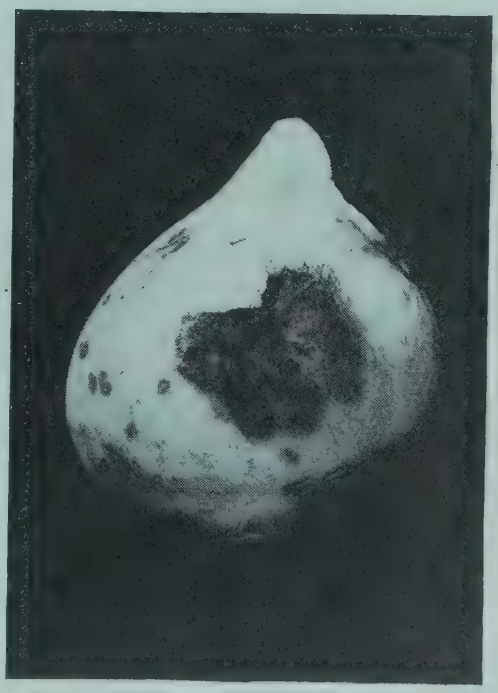

FIG. 41. RESULT OF ARTIFICIAL INOCULATION

Lesion on dormant bulb. The bulb was injured at the point of inoculation. Natural size

mycelium from a culture of the onion Botrytis, *B. Allii* Munn, and with a large sclerotial form of Botrytis from tulips — not *B. Tulipae*. From both of these inoculations a strong infection resulted on the leaves and a slight infection on the stem, in the uninjured as well as the injured plants. A similar experiment with mycelium from the same cultures was tried on onion bulbs, and here *B. Tulipae* produced no infection, while the other two species produced a strong infection, but only on the injured bulbs. It is interesting to note here that on the uninjured bulbs inoculated with *B. Tulipae*, peculiar depressions appeared in the bulb scale that at first seemed to be slight infections. However, microscopical examination showed that the mycelial threads had not penetrated. They were merely superficial. Nevertheless, beneath the mycelium some epidermal cells and other deeper-lying cells had been killed. Microscopical sections of the injured bulbs showed mycelium in the punctures made by the scalpel. It had not, however, penetrated laterally into the tissue, although some of this tissue had been killed.

FIG. 42. RESULT OF ARTIFICIAL INOCULATION
The whole top is involved. Natural size

Inoculation of narcissus.— The result obtained on the narcissus was similar to that on the onion: strong infections appeared on the leaves and slight ones on the stems when the inoculation was performed on

mechanically injured plants. Uninjured plants were not infected. When conidia were used to inoculate narcissus, there was no sign of resultant injury, and microscopical examination of the epidermis showed the conidia to be present but not germinated.

Inoculation of hyacinth.— Detached hyacinth leaves were inoculated with conidia from pure culture. On the fifth day after inoculation, small, yellowish, depressed spots appeared. Microscopical examination of these spots showed an abundance of germinated conidia but no penetration of the epidermis by their germ tubes. Moreover, the tissue beneath the epidermis showed no mycelium.

Inoculation of crocus.— Slight infections were caused on mechanically injured crocus leaves by mycelium of *B. Tulipae*, but no infection occurred on uninjured leaves. A large sclerotial Botrytis from tulip caused no infection in either case. Very slight infections were produced on the papery scales of crocus bulbs. On injured bulbs, all the five inoculated were infected; on uninjured bulbs, only one out of five was infected. Microscopical sections of these lesions showed mycelium ramifying through the tissue, and disintegration of the cells was observed.

Discussion of parasitism

It is evident from these pathogenicity experiments that *B. Tulipae* is practically restricted to tulips. Although under certain conditions it attacks some closely related plants, even such infection occurs, almost invariably, only when there is an injury made at the point of inoculation. Furthermore, a large number of injured plants failed to become infected. When we consider the ease with which the tulip may be infected, whether mycelium or conidia be used as inoculum and whether the host plant be injured or uninjured, these apparent exceptions only make more evident its restricted parasitism. Indeed the writer believes that in those instances in which *B. Tulipae* is reported on other hosts, if the fungus were really that species, the infection took place on an injured part of the host plant. On the other hand, the pathogene shows gradation in parasitism in its feeble attempts to invade plants other than its normal host. First, there are plants such as the crocus, on which are produced only slight infections which do not spread. Next, there are plants such as the narcissus and the onion, on which the conidia do not even germinate and infection

by mycelium can begin only at an injured place. Again, there are plants such as the hyacinth, on which the conidia will germinate and cause local injury, without actually invading the plant. Finally, there is the tulip, in the case of which infections take place easily on uninjured plants.

While this series is too incomplete to be conclusive, the tendency shown is clear, and further experiments in this direction would probably furnish additional evidence of the very limited range of the parasitism of *B. Tulipae.*

Life history

Primary inoculation and infection

The fungus survives the dormant period of the bulb as mycelium or sclerotia and is planted with it in the fall. When the bulb starts into activity in the spring, the fungus starts also and sometimes spreads throughout the entire outer scale of the bulb. If the original infection is near the apex of the bulb, the shoot also is involved in the lesion and the mycelium growing from the bulb tissue infects the leaf tissue. This condition was frequently encountered in studying the disease and is well illustrated in figure 27. Usually it is only the outer, sheathing leaf that is diseased, although sometimes the whole shoot may be affected and fail to emerge from the soil. After growing in the leaf for a time, the mycelium emerges from the dead tissue and, if favorable conditions prevail, conidiophores and conidia are produced. These are formed on the aerial mycelium and also arise directly from the mycelium in the leaf. The unspecialized hyphae and the conidiophores which arise from the leaf emerge through the stomata, and in the specimens observed, only one came from each stoma.

Secondary inoculations and infections

The conidia, produced in great abundance on these first-infected leaves, furnish abundant inoculum for secondary inoculations. Although it is not improbable that they are also transported by such other agencies as insects, spattering rain, animals, and man, the conidia are for the most part scattered to the infection courts by means of the wind.

The infection courts may be any part of the tulip plant except the roots. Conidia falling on these parts germinate very quickly under proper conditions. Experiments with conidia in tulip juice and in distilled water

produced successful germination. In the former there was a good development of germ tubes overnight, while in the latter germination took place but the development of the germ tubes was poor. This experiment was conducted at room temperature. The germ tubes penetrate directly, as discussed under the heading *Pathological histology* (page 351) and cause infection. Visible evidence of infection often appears within the short period of twenty-four hours, as was demonstrated in the pathogenicity experiments. Under conditions unfavorable for germination the conidia are able to retain their viability for some time, as the following experiment illustrates.

Tulip material abundantly covered with conidia was collected on June 12, 1917, at Ithaca, New York. It was kept under laboratory conditions and the capacity of the conidia for germination was tested on June 12, June 25, July 12, and August 2. Germination of conidia was obtained at all of these dates except the last. This shows that in a dry condition the conidia retain for several weeks their ability to germinate. The lesions caused by their infections soon enlarge and produce more conidiophores and conidia, which in turn are capable of producing more infections. That these infections are continually taking place is evident from the presence of lesions of various ages on the same leaf (fig. 25).

Conidia may be carried from badly diseased tops to the bulbs, perhaps being washed down by rain. Several specimens were collected which clearly showed this. Incipient lesions were found on both the stalks and the bulbs of such plants, showing how the inoculum works down to the bulbs. These lesions increase in size and sclerotia are produced. When the bulb becomes dormant the development of the lesion is arrested and the fungus is again ready for hibernation. There is no doubt that the sclerotia retain their vitality for a long period. In fact, isolations have been made from sclerotia which have been in a resting state for several years.

Pathological histology

The material was fixed in Flemming's, in chromo-acetic, and in Gilson's fluids, was embedded in paraffin, sectioned, and stained with both Heidenhain's iron alum-haematoxylon and Flemming's triple stain. Some difficulty was experienced in sectioning lesions on the bulbs because of the numerous, large, starch grains present. In order to study the

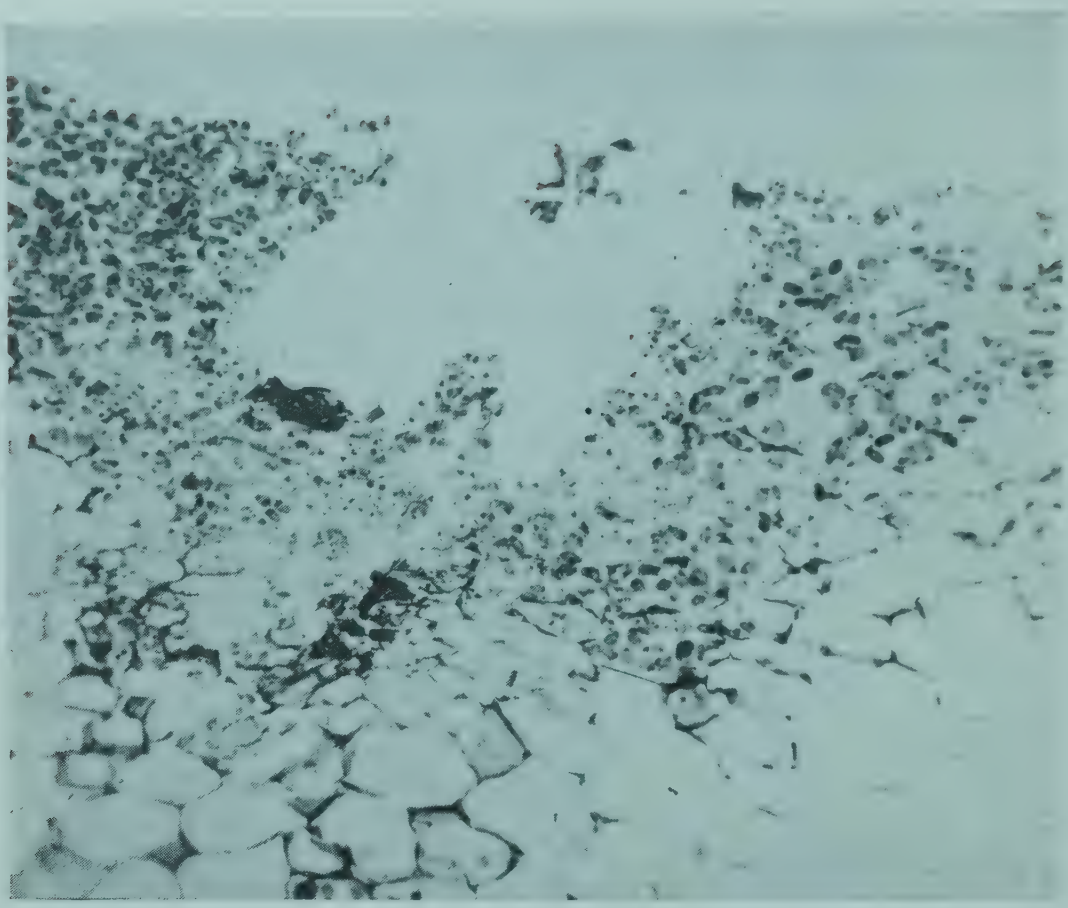

FIG. 43. LESION ON THE OUTER BULB SCALE

Photomicrograph of cross section through lesion. The accumulation of starch in the cells, and an incipient sclerotium, are visible

penetration, certain areas on the tulip leaves were marked with india ink, inoculated by dusting with conidia, and, after various intervals, cut out, killed, fixed, and stained.

On the bulbs, typical necrotic lesions appear, which show a peculiar accumulation of starch about the diseased area. This is pictured in its general features in figure 43, and in more detail in figures 44 and 45, one of which shows a diseased area and the other a healthy one. These starch grains are heart-shaped and large. They react to iodine in potassium iodide in the usual way, and with Flemming's triple stain are colored a beautiful pink. Why they should accumulate in this manner about the lesion is not known.

The mycelium in the bulbous tissue is usually of small diameter and is both inter- and intracellular. Usually in that part of the tissue where the mycelium is advancing and the cells are not yet killed, it is intercellular, while in the older part of the lesion the hyphae penetrate into the cells as well as between them. The protoplasm of the cells at this stage is practically gone. The collapse of these empty cells causes the lesion to be depressed. Sclerotia sometimes form on the surface of the lesion. In figure 43 an incipient sclerotium may be seen.

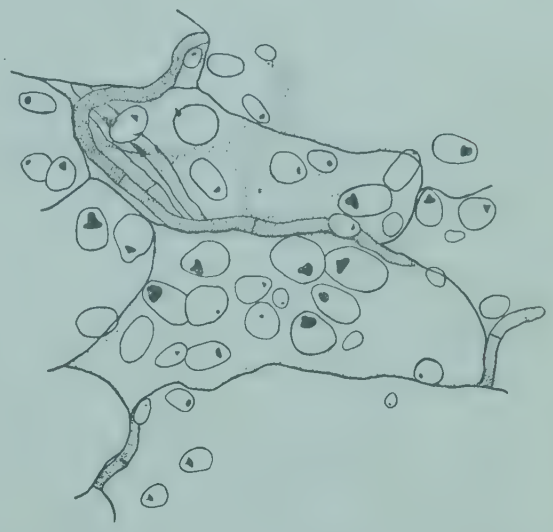

FIG. 44. STARCH ACCUMULATION IN DISEASED TISSUE. × 277

Starch cells in a diseased area of an outer bulb scale, showing numerous starch grains and intercellular mycelium. (Camera-lucida drawing)

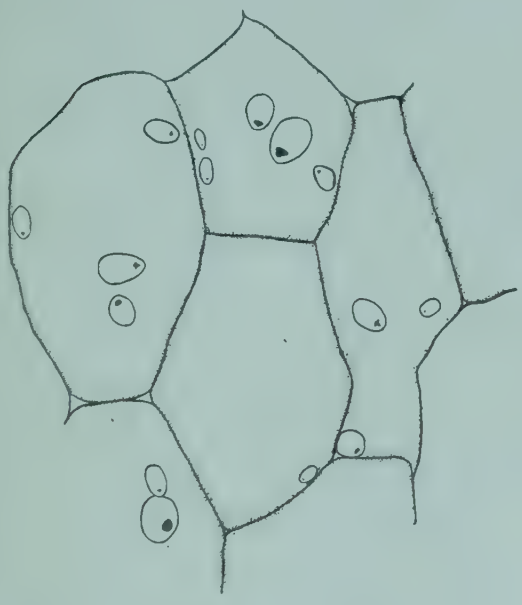

FIG. 45. HEALTHY BULB TISSUE. × 277

The amount of starch shown here may be compared with that shown in figure 44.

Vascular bundles in the bulb scale were markedly affected, and in one case the xylem had entirely disappeared while the phloem, though attacked, still remained in part. In another specimen the bundle had been disintegrated on the side toward the lesion. This involved the phloem, the cells of which stained a deeper blue. There was starch accumulation in this region.

Penetration of the fungus into the leaf tissue has been observed. No appressoria are formed by the germ tubes, which instead penetrate directly through the leaf surface, either through stomata or

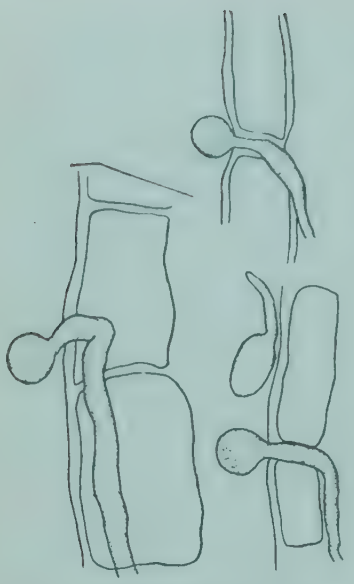

FIG. 46. PENETRATION OF LEAF TISSUE. × 277
Transverse section of epidermis. (Camera-lucida drawing)

between epidermal cells (figs. 46, 47). The germ tubes have not been observed to penetrate directly through epidermal cells. It has been noted that penetration more often occurs where the conidia are more numerous. Probably this is because of the greater enzymatic action, which hydrolyzes the cuticular substance.

The mycelium in the leaf, like that in the bulb, is both inter- and intracellular. This is shown in figures 48 and 49. After the fungus has developed for a time in the leaf tissue, a collapse of the cells results and causes the leaf to become much thinner in the diseased area. Here also, where the mycelium is still intercellular, the cells are not killed. There is injury caused in advance of the mycelium. This indicates the excretion of toxic or enzymatic substances by the pathogene.

The writer thinks that the injury caused in this disease is not due to oxalic acid. Some experiments were made to determine what the nature of the injury from oxalic acid would be. Several plants were injected hypodermically with solutions of oxalic acid of various concentrations, and lesions were produced which strikingly resembled those caused by a fungus. Furthermore, microscopical examination indicated that no fungus had been accidentally introduced. However, the concentrations were necessarily higher than those produced by fungi in culture. The work of Brown (1915) seems to show that neither oxalates nor oxalic acid take part in the toxicity of *B. cinerea*, but

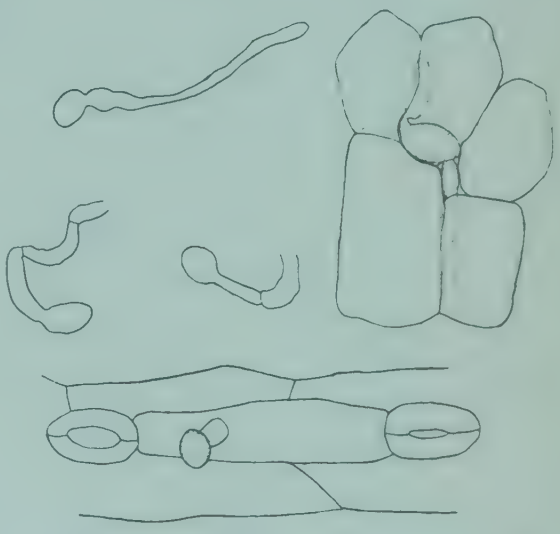

FIG. 47. PENETRATION OF LEAF TISSUE. × 277
Surface view. (Camera-lucida drawing)

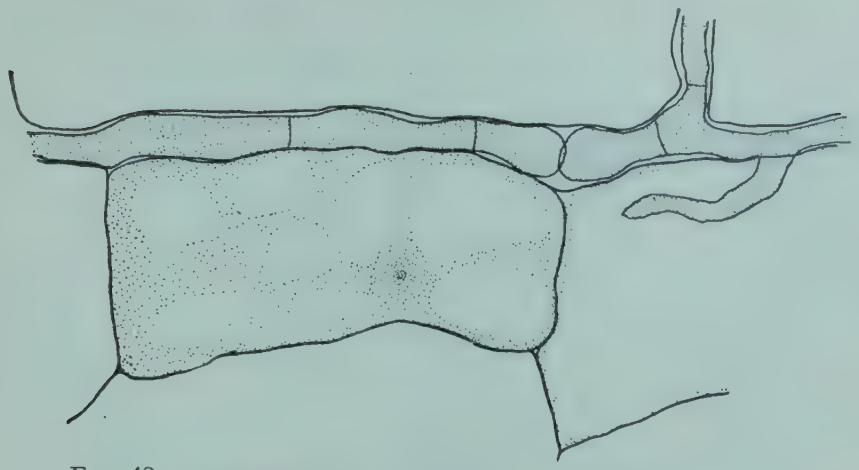

FIG. 48. INTERCELLULAR MYCELIUM IN LEAF TISSUE. × 600
The cells have not yet lost their protoplasm. (Camera-lucida drawing)

that this toxicity is due to enzymatic action.

CONTROL

It has been impossible to carry control experiments far enough to justify making any definite recommendations for the control of *Botrytis Tulipae*. A consideration of the pathogene, however, makes it evident that elimination is probably of first importance. Clean bulbs, free from mycelium and sclerotia, should produce clean tulips, for it is most probable that in these forms the pathogene is carried on the bulbs. Although the disease may possibly be attributed to infested soil, it often occurs on tulips grown in soil in which heretofore no tulips have been grown.

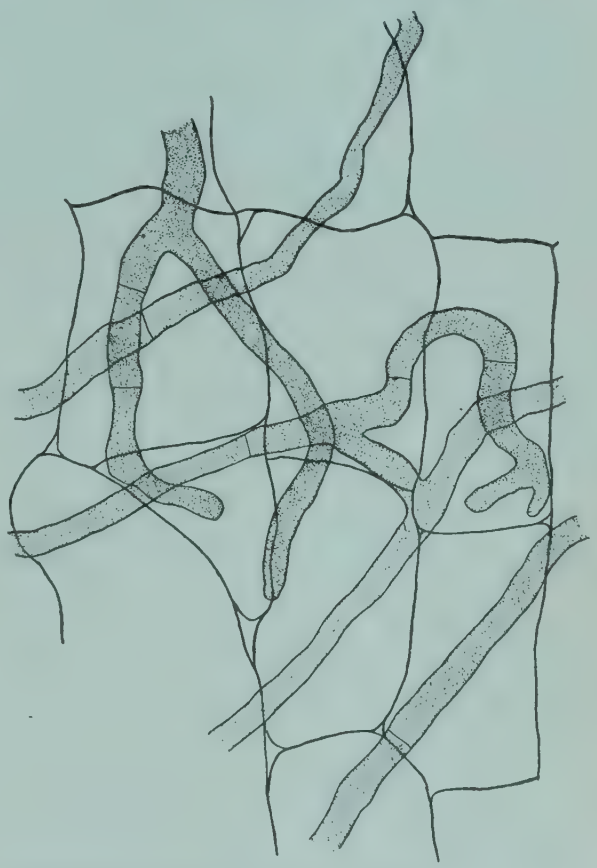

FIG. 49. INTRACELLULAR MYCELIUM IN LEAF TISSUE. × 600
The cells of the leaf are devoid of contents. (Camera-lucida drawing)

FIG. 50. PROLIFERATION OF CONIDIOPHORE. × 840
Showing new branches arising from conidial cluster. (Photomicrograph)

Until further experiments have been made, soil treatment cannot be recommended. Carbolineum has been recommended in the literature as a disinfectant for soil (Elenkin, 1911). Klebahn (1904:33) criticizes this method unfavorably, saying that not even weeds will grow in soil thus treated.

Experiments made at Madison, Wisconsin, in 1917, showed that spraying tulips with bordeaux mixture 5–5–50 caused considerable injury to both the leaves and the flowers, besides giving them an unsightly appearance. Accordingly this treatment is not to be recommended.

From the present knowledge of this disease the following measures seem advisable:

1. Selection of clean bulbs, free from lesions and sclerotia. When the sclerotia occur only on the outer papery scale this should be removed and burned. It is well also to inspect the old stalk of the previous year, if this still remains attached, for it frequently bears sclerotia (fig. 22).

2. Careful handling, to avoid injuring the bulbs, as infection takes place more readily on injured bulbs than on healthy ones.

3. Storage of the bulbs under proper conditions of temperature and humidity. The temperature should be kept as low as possible without injury to the bulbs, preferably about 40° F. The humidity also should be low. These conditions are especially desirable, as they retard the development of any small lesions that may be present on the bulbs at the time of storage, and prevent the germination of any conidia that may be on their surface.

4. Removal and destruction of diseased plants when they appear in the field or the beds. This will limit, if it does not entirely prevent, secondary infections.

SUMMARY

An investigation of the tulip disease caused by *Botrytis Tulipae* (Libert) comb. nov. shows that it is present throughout the United States and that it was probably introduced with the introduction of tulip bulbs. Reports of the disease show that it has been in this country at least since 1901.

Under normal conditions this disease is restricted to the genus Tulipa and within this genus practically all varieties are susceptible. One instance of apparent immunity is the variety Baronne de la Tonnaye, which, during an epidemic of Botrytis blight, showed no evidence of the disease.

Counts made in the spring of 1917, at Ithaca, on one variety of late tulips, Spathulata, showed 100 per cent of the leaves and 98 per cent of the stalks to be affected. Other varieties were similarly infected. These infections were traced to the bulbs, of which the variety Spathulata showed 4.6 per cent with unmistakable Botrytis lesions and the Mrs. Grover Cleveland variety, 5.2 per cent.

The disease is easily recognized on the bulbs when the fungous sclerotia are present in the lesions. On the leaves, the flower stalks, and the flowers, a severe blighting frequently takes place.

Studies of the literature and herbarium specimens show that the disease under consideration is to be ascribed to *Botrytis Tulipae* (Libert) comb. nov.[4]

Cultural studies have demonstrated that both the small sclerotia on the bulbs and the conidial form on the leaves and other parts of the tulip plant are stages of one and the same fungus, namely, *Botrytis Tulipae*.

[4] In recent literature the fungus has gone by the name *Botrytis parasitica* Cavara, but the specific name of Libert has priority.

The morphology of the parasite has been investigated in some detail. The manner of formation and attachment of the conidia has been brought out, microconidia have been demonstrated for this species and conidial measurements show that while the variation in size is from 12–24 x 10–20, the greater number of spores measure 16–17 x 9–10.

Conidial production, which rarely takes place in pure cultures under ordinary conditions, was found to occur abundantly when plate cultures were partially dried. Abundant conidia were also formed on sterilized tulip leaves in large test tubes.

The parasitism of *B. Tulipae* has been fully demonstrated by numerous infections brought about by the use of pure cultures of the organism. Inoculations of other plants, both nearly and distantly related, while showing the parasite to be restricted to tulips, show also that the parasite exhibits a weak and varying degree of ability to attack other plants.

Hibernation is by means of sclerotia which live over the winter on the bulbs. Infection spreads from these bulbs to the developing shoots, where abundant conidia are produced. These primary lesions serve as the source of inoculum for secondary infection. The conidia produced in this manner retain their vitality for several weeks.

Sections through lesions on the bulb show an accumulation of starch about the diseased area. In the penetration of the tissue by conidial germ tubes, no appressoria are formed and the germ tubes penetrate directly through the epidermis or through the stomata.

Although extensive control experiments have not been made, it is recommended that clean bulbs, careful handling of bulbs, proper storage, and systematic removal and destruction of diseased plants in the field will largely hold the disease in check.

Memoir 39, *The Genetic Relations of Plant Colors in Maize*, the sixth preceding number in this series of publications, was mailed on July 19, 1921.

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TYPHA INSECTS: THEIR ECOLOGICAL RELATIONSHIPS

P. W. CLAASSEN

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CONTENTS

PAGE

Ecological studies of Typha 463
The swamp area of the United States 463
Places of study 464
The species of Typha 465
The distribution of Typha 465
Growth habit and reproduction 466
Germination *Typha latifolia* 467
Typha as a commercial asset 470
The insect fauna of Typha 471
Lepidoptera 472
Arzama obliqua Walk 472
Nonagria oblonga Grote 479
Arsilonche albovenosa Goeze 483
Archips obsoletana Walk 485
Lymnaecia phragmitella Staint 487
Dicymolomia julianalis Walk 490
Coleoptera 493
Calendra pertinax Oliv 493
Notaris puncticollis Lec 497
Hemiptera 497
Ischnorrhynchus resedae Panz 497
Siphocoryne nymphaeae Linn 500
Aphis avenae Fab 500
Rhopalosiphum dianthi Schrank 501
Rhopalosiphum persicae Sulz 501
Aphis gossypii Glov 501
Macrosiphum granarium Kirby 501
Hyalopterus arundinus Fab 501
Hymenoptera 501
Aleiodes intermedius Cress 501
Apantales cinctiformis Vier 502
Elachertinae sp 502
Pimpla indagatris Walsh 502
Pimpla inquisitoriella D. T 502
Diptera 502
Platychirus quadratus Say 502
Macrosargus clavis Will 502
Chaetopsis aeneae Wied 502
Sturmia nigrita Town 503

PAGE

Résumé 503
Insect inhabitants of the head of Typha 503
Insect inhabitants of the leaf of Typha 505
Insect inhabitants of the stalk of Typha 506
Insect inhabitants of the rhizome of Typha 507
Literature cited 508

TYPHA INSECTS: THEIR ECOLOGICAL RELATIONSHIPS

TYPHA INSECTS: THEIR ECOLOGICAL RELATIONSHIPS

P. W. Claassen

In order that the ecological relationships of the insect fauna of the cat-tail plant may be better understood, the first part of this paper deals with the ecology of the cat-tail plant. In the second part, the life history and biology of the insect inhabitants of the plant are discussed. This part of the paper has been treated from a systematic point of view, considering the insects under their respective orders, rather than grouping them according to their life habits. In the résumé, composing the third part, an attempt has been made to bring out the true ecological relationships, grouping the insects with reference to the parts of the plant they affect, their relative importance, and their interrelations.

ECOLOGICAL STUDIES OF TYPHA

THE SWAMP AREA OF THE UNITED STATES

According to Davis (1911)[1] there are 139,855 square miles of swamp area in the United States, exclusive of Alaska. This includes bogs, marshes, muck lands, and the more typical swamps. The vegetation in these wet lands varies from the semi-floating forms to the wooded plants of the more solid areas. Needham and Lloyd (1916) state that the bogs, marshes, and swamps "occupy a superficial area larger by far than that covered by lakes and rivers of every sort. They cover in all probably [*sic*] more than a hundred million acres in the United States."

Much of the vegetation of this wet area consists of cat-tail (Typha). Many of the marshes contain an almost pure growth of cat-tail, as, for example, the Montezuma Marsh at the foot of Cayuga Lake. This marsh covers an area of approximately 36 square miles. Although it is impossible to give definite figures on the size of the area occupied by cat-tails in the United States, it is safe to say that there are thousands of square miles of wet lands which are covered by either a pure growth of cat-tail or plant associations in which the cat-tail is the dominant form.

Author's acknowledgment. The author is indebted to Professor James G. Needham for his helpful suggestions and criticism in this work.

[1] Dates in parenthesis refer to *Literature cited*, page 508.

PLACES OF STUDY

These studies have been made largely from material gathered in the swamps and marshes around Ithaca, New York, especially from Renwick Marsh, at the head of Cayuga Lake. Other collecting places around Ithaca were Michigan Hollow, Mud Creek Swamp, near Freeville, the McLean Bogs, Vanishing Brook, north of the Cornell University campus, Cascadilla Creek, and various other places, wherever cat-tails were found growing. Observations were made also on the extensive cat-tail marshes of Lake Ontario, at North Fairhaven. During the season of 1916-1917, studies on cat-tails were made also in the vicinity of Lawrence, Kansas.

The Renwick Marsh comprises a field of many acres, of which a large proportion is covered with cat-tail. In some places, this plant grows so thickly that all other vegetation is excluded, and especially is this true of the central part of the marsh, where the soil is much wetter. As one approaches the outer margin, other plants mingle with the cat-tails; and at the border, where conditions are drier, the cat-tail growth is sparse. All the cat-tail patches along the Inlet Valley, up to the Buttermilk Falls region, are referred to as the Renwick Marsh.

Michigan Hollow is a swamp located about six miles from Ithaca, in the Inlet Valley. Cat-tails grow here only scatteringly, in small but rather dense patches. This swamp was visited several times to make collections and observations.

In the McLean Bogs, cat-tails are not found in large numbers, but since these bogs were visited every Saturday throughout the spring and summer of 1916, the author was enabled to make more careful and complete observations of the conditions and life histories of the insects of the cat-tail plants there found. Moreover, where cat-tails are not so abundant, a higher percentage of infestation usually occurs, which renders it much easier to obtain material and to make comparative studies.

The Mud Creek Swamp is an old swamp extending along Mud Creek, near Freeville. Here, also, the cat-tails grow but sparingly, but it was found easy and convenient to make frequent observations and collections of material.

Along Vanishing Brook, north of the Cornell University campus, there are a number of small patches of swampy ground, on which cat-tail plants

may always be found. On account of its nearness to the laboratory, this was found to be a convenient place to make some of the observations.

Occasional cat-tail plants are also found in Bool's Back Water and in Cascadilla Creek, two places which were likewise chosen for study because their close proximity to the laboratory made daily observations possible.

THE SPECIES OF TYPHA

According to Britton and Brown (1913) there are about ten species of Typha in the temperate and tropical regions of the world. In the United States there are at least two species represented, *Typha latifolia* L. (type species) and T. *angustifolia* L. Dudley (1886) lists *T. latifolia* L., var. *elongata*, n. var., as a variety occurring in New York. He describes it as follows: "Leaves very numerous, dark green, elongated (2–3½m.) and fruiting spike elongated, often 30 cm."

Typha latifolia has broad leaves. The staminate and pistillate parts of the flower spike are contiguous. The stigmas are spatulate or rhomboid. Pollen grains occur in fours. Pistillate flowers are without bractlets.

Typha angustifolia has narrower leaves than *Typha latifolia*. The staminate and pistillate flowers of the flower spike are usually separated by a short interval. The stigmas are linear or oblong-linear. Pollen occurs in simple grains. The pistillate flowers have bracts.

Typha is known by the following common names: cat-tail, great reed mace, cat-o'-nine-tail, cat-tail flag, cat-tail rush, flax tail, blackamoor, blackcap, bullsegg, bulrush, watertorch, and candlewick. The names "marsh beetle" and "marsh hog" have also been applied to the Typha plant.

THE DISTRIBUTION OF TYPHA

Cat-tails are common in the temperate and tropical regions of America, South America, Europe, and Asia. Wherever favorable soil conditions occur, cat-tails will be found growing; even a spring on the hillside or the outlet of a drain pipe will sometimes support a few of the plants. Large patches of them grow in the Rocky Mountains, at an altitude of 7500–8500 feet. *Typha latifolia*, the commonest of all the species, occurs throughout the United States in any favorable location. *Typha latifolia* grows abundantly throughout North America, except in the extreme

North. *Typha angustifolia* grows abundantly in the marshes along the Atlantic Coast from Nova Scotia to Florida, as well as inland and even in California.

GROWTH HABIT AND REPRODUCTION

Cat-tails are marsh or aquatic plants, with creeping rootstocks, fibrous roots, and glabrous, erect stems. They are perennial plants, the rootstocks remaining alive while the stem dies down to the ground every year. The following spring these rootstocks, or rhizomes, send up the new plants. Plants which attain only partial growth during the season keep the center alive that winter and probably reach maturity the following summer. The rhizomes spread in every direction and within a few years a large group of cat-tails results from the offsets of a single plant. It is really very difficult to define the limits of a single plant, since they are so linked together by these underground rhizomes (Plate XLV, 56). A two-years growth of a plant, with the connecting rhizome and the offset which will form the next season's stalk, is shown in Plate XL, 18.

Aside from the vegetative mode of increase, Typha produces a great number of seeds each year. These seeds are provided with pappus, which carries them far abroad and insures seeding in all possible situations. In *The Book of Nature Study* (Farmer, 1902-10), the following statement occurs: "When they [the fruits] become detached from the spike, the hairs borne by the stalk of each fruit act as wings to disperse the seed: the hairs fluff out into downy masses, so that the whole spike looks about a hundred times as large, for a single head will contain a quarter of a million of these flying seeds, according to Professor Lloyd Praeger's estimate."

In order to determine somewhat accurately the number of seeds produced by one head of *Typha latifolia*, the number of seeds in four dry, mature heads was determined. For this work an analytical balance was employed. The procedure was as follows: First, each head was weighed entire; then a small bunch of the seeds was detached and weighed, after which the number of seeds in this bunch was counted; finally, all the seeds were removed and the rachis alone was weighed. From the figures so obtained, the number of seeds in each of the heads was computed (table 1), and the number of seeds in the average Typha head was found to approximate 250,000.

TABLE 1. COMPUTATION OF THE AVERAGE NUMBER OF SEEDS IN EACH TYPHA HEAD

	Sample 1	Sample 2	Sample 3	Sample 4
Length of head (millimeters)	160	180	180	160
Weight of entire head (grams)	35.6735	30.5632	35.2700	27.1150
Weight of rachis (grams)	2.8330	1.9480	2.1610	1.6850
Weight of seeds minus rachis (grams)	32.8405	28.6152	33.1090	25.4300
Weight of detached bunch of seeds (grams)	0.0179	0.0490	0.0400	0.0400
Number of seeds in detached bunch	167	480	300	295
Estimated total number of seeds in head	306,393	280,320	248,317	187,546

Average number for the four heads, 255,644.

GERMINATION OF TYPHA LATIFOLIA

The manner of germination of *Typha latifolia* is very unusual. The development of the plant from the seed was observed in the laboratory. The seeds were placed in watch glasses and could thus be studied under the binocular microscope from day to day. Some of the watch glasses contained only water in which the seeds germinated, while in others a little soil was placed in the bottom in order to observe the growth of the roots. The watch glasses were kept covered to prevent evaporation. The seeds, when first thrown upon the surface of the water, remained floating. Soon, however, the pericarp broke open and the little seeds sank to the bottom.

The seeds are much elongated, pointed at one end and at the other closed by a cone-shaped trapdoor, or cap (Plate XXXIX, 3). The general appearance of the seed is not much unlike some of the insect eggs which are closed at one end with a capsule-like cover. Ten seeds of *T. latifolia*, chosen at random from two heads, were removed from the pericarp and the length and diameter of each was carefully measured (table 2). The average length of the seed was found to be 1.339 millimeters, and the average greatest diameter, 0.307 millimeter. The surface of the seed is sculptured with small, branching ridges, starting at the end of the cap and branching as they run down to the other end. The entire seed, including both its pericarp and its pappus, is about 10 to 12 millimeters long. The pappus consists of from 15 to 20 white hairs, attached to the base and lower quarter of the stalk (Plate XXXIX, 1 and 2).

TABLE 2. MEASUREMENTS OF THE SEEDS OF TYPHA LATIFOLIA

Specimen	Length (millimeters)	Diameter (millimeters)
1	1.50	0.29
2	1.21	0.25
3	1.42	0.28
4	1.35	0.28
5	1.42	0.37
6	1.05	0.28
7	1.42	0.37
8	1.42	0.37
9	1.45	0.28
10	1.15	0.30
Average	1.339	0.307

When germination begins, the cotyledon lengthens and pushes out through the trap door. Sometimes the cap is carried away on the tip of the developing embryo, but more often it remains attached as if by a hinge to the seed. The embryo, immediately after emerging from the seed, turns downward toward the bottom of the dish. Growth is very rapid. Hardly has the embryo come out of the seed before the epidermal cells near the tip begin to send out slender root-hairs, which help to fix the plant to the bottom soil. The other end of the embryo, or cotyledon, remains in the seed, absorbing the reserve starchy material, the only food of the young, developing embryo (Plate XXXIX, 5). When the embryo has become about twice or three times the length of the seed, the growing tip pushes out the first root (Plate XXXIX, 8). The root also bears a number of the root-hairs. With the exception of the ones at the tips of the roots, these root-hairs disintegrate as the plant further develops. At about the same time that the first root appears, the formation of the second leaf may be seen at the crown of the young plant (the outpushing embryo or cotyledon is considered the first leaf). This second leaf soon penetrates the epidermal cells of the first leaf, and comes out to grow and function as a true leaf (Plate XXXIX, 9). After all the food material in the seed has been absorbed, the tip of the first leaf either disintegrates and is thus loosened from the seed, or the tip of the leaf is withdrawn from the seed (Plate XXXIX, 10). The successive stages of the growth of the plant are shown in Plate XXXIX, 4–10.

Not every seed in the head of *Typha latifolia* is perfectly formed or fertile. A number of them never become fully mature, and therefore could not possibly germinate. It is an easy matter to distinguish the fertile seeds in a mature head from the sterile ones. The mature fertile seeds lie in a closely fitting pericarp, while the sterile ones are inclosed in a pericarp which is developed to more than twice the natural size and which has a "hollow" interior with the kernel undeveloped (Plate XXXIX, 1).

In order to determine the approximate percentage of fertility in the seeds of *Typha latifolia*, a number of seeds were picked off at random from several heads and by a careful examination the number of fertile and sterile seeds was determined. The results of these counts are shown in table 3, where it appears that about 75 per cent of the seeds on the mature heads are fertile. The heads from which these counts were made were picked at random and should represent about average conditions. The third head had nearly half of the seeds sterile; the fourth, however, had a high percentage of fertile seeds.

TABLE 3. DETERMINATION OF THE APPROXIMATE PERCENTAGE OF FERTILITY OF TYPHA SEEDS

Head	Number of seeds counted	Number of seeds fertile	Number of seeds sterile	Per cent fertile
1	300	233	67	77.7
2	200	156	44	78.0
3	250	140	110	56.0
4	250	211	39	84.4
Total	1,000	740	260	.....
Average per cent fertile	.....	.....	.....	74

Having thus ascertained the approximate percentage of fertility in the seeds, experiments were conducted to determine the percentage of germination of the fertile seeds. The seeds were placed in covered watch glasses, and, though kept in the light, were protected from direct sunlight. Germination commenced within a few days after the seeds had been placed in the water. Careful counts were made of the number of seeds

that germinated in each of the watch glasses. The results are shown in table 4. These figures would indicate that not more than two-thirds of the fertile seeds germinate under experimental conditions. Calculating, then, from the percentage of fertility and the percentage of germination, as given in tables 3 and 4, a head containing 250,000 seeds might actually give rise to 125,000 new plants — a 50-per-cent efficiency in reproduction.

TABLE 4. DETERMINATION OF THE PERCENTAGE OF GERMINATION OF FERTILE SEEDS

Head	Number of seeds	Number of seeds germinated	Number of seeds sterile	Percentage of germination
1	20	12	8	60.0
2	50	34	16	68.0
3	18	12	6	66.6
4	73	37	36	50.6
Total	161	95	66	.....
Average per cent germinated	.....	.....	.....	60.5

TYPHA AS A COMMERCIAL ASSET

The vast areas of cat-tail have as yet been little utilized. The plant is rich in starch and other food values and grows in situations now regarded as waste lands. It would yield great quantities of supplies, if only a definite use for it could be found. The Indians and a few other races have used cat-tail products for various purposes. Hooker (1876) says:

> The starchy rhizome of Typha possesses slightly astringent and diuretic properties, which led to its use in East Asia for the cure of dysentary, urethritis, and aphthae. The stems and leaves are used for thatching cottages. It has been vainly tried to utilize the bristles of the spike in the manufacture of a sort of velvet. [The pollen of Typha is made into bread by the natives of Scind and New Zealand.]

Engler and Prantl (1889) say: "The rhizome, rich in starch, may serve as food material; the leaves of several species are used for weaving. The pollen, which is easily recognized by the occasional tetrads, serves at times as surrogate for lycopodium powder."[2]

[2] Translation from the original German.

Parker (1910) speaking of the plants used for food by the Indians, says: "The roots of the cat-tail were often used. Dried and pulverized the roots made a sweet white flour useful for bread or pudding. Bruised and boiled fresh, syrupy gluten was obtained in which corn meal pudding was mixed."

Muskrats are very fond of the rhizomes of the cat-tail, and in the cat-tail swamps the muskrats are accordingly found in large numbers. The leaves of the cat-tail are used to some extent in the manufacture of barrels. On account of their spongy structure, the dried leaves, placed between the staves, expand greatly when moistened, thus making the barrels water-tight. The leaves are also used for chair bottoms. (Dudley, 1886).

The rich starch content of the plant is especially concentrated in the rhizomes, where the cells of the rhizome core (Plate XLV, 57 and 60) are completely filled with small starch granules. This is true of the rhizomes in their dormant or winter conditions (Plate XL, 13). If, however, one examines the cells later in the season, after the plant has attained a growth of several feet, the cells are found to be only partially filled with starch granules, much of the starch having been used up in the rapid early growth of the plant (Plate XL, 15). This fact, showing that they have a much greater concentration of starch during the dormant season than during the growing season, has a direct bearing upon the possible uses of the rhizomes, and any attempts made for the utilization of the starch should be made on the dormant rhizomes. The possibility of utilizing the Typha plant as a source of food has been discussed by the author in another paper (Claassen, 1919).

THE INSECT FAUNA OF TYPHA

The insects which are found on cat-tail have not hitherto been studied as a group. Most of them have been recorded as inhabiting cat-tail, but very little has been published on their detailed life histories and ecological interrelations.

The following discussion includes only those insects which have been found on cat-tail and studied during the course of this investigation. It includes six species of Lepidoptera, two of Coleoptera, eight of Hemiptera, five of parasitic Hymenoptera, and four of Diptera.

LEPIDOPTERA[3]

Arzama obliqua Walk.

Arzama obliqua Walk., a moth of the family Noctuidae, has been known in the adult stage for more than half a century. The species occurs throughout eastern United States and Canada, its host plant being *Typha latifolia*. In New York, near Ithaca, the writer has taken specimens from the following places: Michigan Hollow, Renwick Marsh, Bool's Back Water, McLean Bogs, Cascadilla Creek, and Ringwood Hollow.

Life history and habits

The life history of this insect is unusual and interesting from an ecological point of view. There is only one generation a year. The full-grown larva passes the winter in its burrow in the plant.

Egg-laying.— The eggs are laid on the surface of one of the first-formed leaves of *T. latifolia*, from six to fifteen inches below the tip. This later becomes one of the outer leaves of the plant. The eggs are placed on the leaf several layers deep. The lower layer covers the largest area and contains from twenty-five to forty eggs, while the upper layers cover only the central part of this bottom layer, forming a gradually sloping mass and containing from ten to twenty eggs in the two or more upper layers. The total number of eggs in one egg mass varies from thirty-five to sixty. The whole egg mass is covered with a thick layer composed of a mixture of froth, hairs, and scales from the body of the female. The egg mass greatly resembles a mass of spider's eggs (Plates XLI, 24 and 25, and XLVI, 65). It is of a dirty, yellowish-white color. It measures from twelve to fifteen millimeters in length, from seven to ten millimeters in width, and from three to four millimeters in height at the center. In shape it is oblong and convex, the edges gradually thinning out and adhering closely to the surface of the leaf. The long axis of the egg mass corresponds to the long axis of the leaf.

One female apparently lays several egg masses. In dissecting out the ovary of one female, 225 eggs were found, all fully formed and developed; and since only thirty-five to sixty eggs occur in a single mass, this indicates that one female may deposit about half a dozen egg masses.

[3] The Lepidoptera mentioned in this paper have all been determined by Dr. W. T. M. Forbes.

Usually only one egg mass occurs on the same leaf, but sometimes two, and in one instance three, masses were found on a single leaf. It is not uncommon to find two or three leaves of the same plant with an egg mass on each of them.

In the spring of 1918, careful observations were made for the appearance of the adults or the egg masses on the plants. In the laboratory, where moths had been bred, they failed to mate or to deposit eggs in the characteristic manner. A few females did lay infertile eggs on the stems and leaves of Typha. Egg masses were first noticed in the field on May 26. After this date new egg masses were constantly found until June 8. The height of egg-laying was between May 26 and June 2. At the McLean Bogs the egg masses appeared about six days later than those at the places around Ithaca.

The larva.— On turning the egg mass over, after the larvae have hatched, the empty egg shells are disclosed. The hatching process does not disturb the egg mass in the least. Without devouring the egg shell, the embryo breaks through it and bores directly into the leaf of the cat-tail, where it works as a leaf miner. This manner of hatching seems to be an excellent protective adaptation against egg parasites and other enemies. The mass is practically impervious to water. Thus from the time the egg is laid to the time when the larva hatches and enters the leaf to become a leaf miner, it is not once exposed to the direct dangers of enemies or of weather conditions.

Once the larvae enter the leaf, they begin their work as typical leaf miners. The structure of the leaf of the cat-tail plant is rather peculiar. The fibro-vascular bundles are found mainly in longitudinal, I-like partitions. This produces a loose inner structure with many large air spaces (Plate XL, 11). The longitudinal partitions are again traversed by transverse partitions which also are composed of parenchyma. A leaf of Typha with the epidermis removed to show this inner structure appears in Plate XLV, 58. When the larvae have entered the leaf, they begin to mine, mostly downward, scraping off the chlorophyll from the upper and lower epidermis of the leaf. They eat out the transverse partitions, leaving the longitudinal partitions and the fibro-vascular bundles undisturbed except when occasional larvae cut through to get in other channels. A few of the larvae may first mine upward toward the tip of the leaf, but soon they all proceed downward, moving abreast along the

channels. As many as eight larvae have been found together in one channel. It is probably due to such a crowded condition that a larva occasionally crosses over into another channel.

After the larvae have mined down for a distance of twenty to twenty-four inches, they molt in the mines and immediately afterward leave the mines through a little exit hole which is usually made on the inner side of the leaf. As soon as the larvae appear on the surface of the leaf they at once seek shelter, usually continuing down the stem of the plant and crawling behind the sheath of one of the outer leaves.

Since the larvae later become true stem borers, the question arises why they should come out of the mines of the leaf ten or fifteen inches away from the stem instead of remaining in the mines and working down the leaf until they reach the stem and can enter it directly. There are two plausible reasons against such behavior: first, the larvae later become solitary borers and after coming out of the leaf they separate and individually enter the stems of different plants; second, the width of the head of the second-instar larva exceeds the width of the average longitudinal channels in the cat-tail leaf. Careful measurements of the molted heads of the first-instar larvae and measurements of the width of the average channel of the leaf showed that the width of the head during the first instar was only slightly less than the width of the channel. The width of the heads of the second instar was considerably wider than the width of the channels of the leaf. Following are the average measurements:

Width of head of first-instar larva.....	0.597 millimeter
Width of head of second-instar larva.....	0.90 millimeter
Width of channel in leaf.....	0.62 to 0.72 millimeter

It would therefore be impossible for the larvae to remain in the leaf after the first molt unless they widened the leaf by taking out the longitudinal fibrous partitions.

Although the larvae ultimately become solitary stem borers, they do not always scatter immediately after emergence from the mines and bore directly into the stems of the plant. In one instance, on June 29, 1916, it was found that a whole contingent of larvae had migrated to the head of the plant, where they found shelter behind the leaves that were sheathing the flower spike. Here they were feeding on the staminate flowers. A few days later they had all descended and scattered to different

plants. It is probable that such a migration to the flower spike was accidental; on the other hand, it may have been because the plant had a central stalk with a flowering spike that the larvae could not or would not enter it, for the writer has never found that they bored into a plant which had a flower stalk, nor has he ever found a plant in which the stem borers occurred producing a flower stalk.

The larvae enter the stalk from behind the sheath after they leave the leaf, and there they feed for some time. Only once were two larvae found in the same burrow. They normally become solitary borers, tunneling through the center of the stem, going downward to the crown, and sometimes even advancing for a short distance into the rhizome. This tunneling causes the central leaves of the plant to die, and consequently no flower spike is formed. The affected plants are easily recognized by the presence of the dead central leaves.

The larvae grow rapidly and by late fall have attained a length of nearly two inches. They leave the burrow full of the frass and the shreds of the fibrous tissue torn loose by their passage. In the fall, before the larvae go into hibernation, they eat out an exit hole in the stem, four to six inches above the ground, which they loosely plug up with frass and fibrous material. They then make a little compartment, or cell, by closing the burrow above and below with a mass of frass and fibrous material, as shown in Plate XLI, 27 and 28, and thus pass the winter. If one visits the marshes in winter and opens the plants, the larvae are found in the burrow, completely surrounded by ice. Larvae taken to the laboratory during September and October and placed in metal salve boxes on moist, sterilized sand, pupated in February and March. Adults emerged from sixteen to twenty days later. Larvae brought into the laboratory in the spring pupated much later, as is shown by table 5.

In the laboratory, several days before the larva transforms to the pupal stage, it begins to spin a thin, irregular layer of fine thread all over the surface of the sand in the salve box. In the field, one finds these loose webs lining the burrows in the stalks. The larva then becomes very sluggish and gradually shortens until it seems only about half of its normal length. The shiny, almost black, larval skin becomes much lighter in color. This is a sign that pupation will occur within twenty-four to

thirty-six hours. When the larva is ready to pupate, the larval head splits along the epicranial suture and the skin breaks open on the median dorsal line, along the first two thoracic segments, extending also about three-fourths of the way across the third thoracic segment. Gradually the skin slips off backward until the newly formed pupa is free. The pupa is at first entirely white except the cremaster, which is dark brown.

TABLE 5. LENGTH OF PUPAL PERIOD OF ARZAMA OBLIQUA

Specimen	Date of pupation	Date of emergence	Sex	Length of pupal stage (days)
1	February 21	March 11	Female	18
2	March 4	March 22	Male	18
3	March 10	March 29	Female	19
4	March 21	April 7	Male	17
5	March 25	April 11	Female	17
6	March 25	April 12	Female	18
7	March 25	April 11	Female	17
8	March 26	April 12	Female	17
9	March 28	April 14	Female	17
10	March 29	April 14	Male	16
Average length of pupal stage				17.6

TABLE 6. MEASUREMENTS OF PUPAE OF ARZAMA OBLIQUA*

Specimen	Females		Males	
	Length (millimeters)	Width (millimeters)	Length (millimeters)	Width (millimeters)
1	33.0	7.0	29.0	7.0
2	35.0	8.5	28.5	6.5
3	31.5	6.5	28.0	6.5
4	30.5	7.5	.....	.....
5	31.5	6.8	.....	.....
6	35.5	8.0	.....	.....
7	33.0	7.0	.....	.....
Average	32.85	7.25	28.5	6.7

*The measurements of the pupae of *Arzama obliqua* were taken as follows: length, from the anterior end to the tip of the cremaster; width, the greatest lateral width of the pupa.

The first color of the body appears on the dorsal surface of the meso- and metathorax and on the first and second abdominal segments. After about ten minutes more the entire abdomen begins to assume a reddish color, the thorax, head, and wings still remaining nearly white, however. The pulsation of the dorsal vessel is very noticeable at this time. At the end of another twelve minutes the color is darkest on the sixth, seventh, and eighth abdominal segments, being more pronounced on the dorsal surface. Twelve minutes later the head begins to show color. In another half hour the entire pupa, except the wings, has become a reddish brown in color. The wings, which remain white the longest, now begin to show a little color. Later the pupa turns very dark brown, almost black.

Description of the stages

The egg

Light yellowish in color; round, though somewhat flattened, with the micropyle on the upper side, away from the surface of the leaf (Plate XLI, 21). 1 to 1.2 mm. in diameter and 0.8 mm. in height. Sculpturing very fine but quite characteristic; micropyle represented by a small dot surrounded by a rosette of about twelve elongate cells. This surrounded in turn by two other rings of more or less elongate cells; a reticulation following, with cells more or less regularly hexagonal; and, finally, the outside cells slightly elongated transversely. Entire reticulate area around the micropyle covering about two-thirds of the upper surface of the egg. Remainder of egg sculptured with a number of small tubercles, some occurring in lines so as to suggest circumferential bands of tubercles.

The first-instar larva (Plate XLI, 29)

Length 3.43 mm., width 0.58 mm. across the head. Head light brown, labrum and eyes darker. General color white, with a median purplish stripe. Spiracles on the eighth abdominal segment very large and dorsally located, as in the full-grown larva. After larva has been feeding for a few days, general color yellowish green.

The full-grown larva (Plates XLI, 22, and XLVI, 66)

Length 50 to 60 mm., width 6 to 7 mm. General color shiny muddy black. Head very dark brown. Lower half of clypeus light yellow. Basal knobs of antennae light grayish yellow. Labium light gray. Thoracic shield the same color as the head. A light median line along the length of the prothorax. Individual segments of the body darker posteriorly. A dark median line along the dorsal surface of the entire larva. Ventral surface of the larva much lighter, being whitish gray in color.

The larva appears very much like a typical noctuid larva except for the position of the spiracles of the eighth abdominal segment. The spiracles on the other segments of the body occur in the natural place,

but the spiracles of the eighth segment have migrated from the lateral margin to a position on the posterior margin of the dorsal surface as shown in Plate XLI, 30. The ninth abdominal segment consequently is much smaller, being only about half as thick dorso-ventrally as the other segments. This better adapts the larva to live in its burrow in a plant where an excess of moisture occurs. It is not at all uncommon to find a larva entirely submerged in the water with the exception of these large spiracles, which protrude above the surface of the water. These two spiracles are more than twice as large as the other abdominal spiracles.

The arrangement of the tracheal system in the larva is shown in Plate XLI, 31. It consists of two main longitudinal tubes, which originate from the spiracles of the eighth abdominal segment and extend as far forward as the first thoracic segment, where they are united by a transverse trunk. From this transverse trunk arise the tracheal tubes of the head. Paired spiracles are present on the meso- and metathorax and on the first eight abdominal segments. All of these spiracles are functional except those of the metathorax, which are much reduced and seem almost vestigial. Each of the spiracles, except those on the eighth abdominal segment, are connected with the main tracheal trunk of the body by small tubes, the tubes on the metathoracic segment being reduced to mere threads. Most of the tracheal branches of the body take their origin from the longitudinal trunk, near its junctions with the spiracles. From the thoracic spiracles, only small, branching tubes originate. From the first abdominal spiracle a large tracheal tube originates from the tube joining the spiracles to the longitudinal trunk, and smaller branches spring from the trunk. Segments 2, 3, 4, 5, and 6 of the abdomen each have a pair of large tubes arising from the main trunk just above the spiracles. These tubes branch out into two parts, as shown in Plate XLI, 31. Segment 7 of the abdomen has a number of smaller branches, and segment 8 has a number of still smaller branches in front of the large spiracles.

The pupa (Plate XLI, 23)

Female, average length 32.85 mm., width 7.25 mm., male, length 28.5 mm., width 6.7 mm. Head, thorax, and appendages black. Abdomen dark brown. Frontal prominence very weak. Wings extending back over two-thirds of the fourth abdominal segment. Prothorax about two-fifths of the length of the metathorax. Surface of the head and thorax rugose. Clypeo-labral suture very distinct. Labium distinct, the labial palpi nearly twice as long as labium. Maxillae extending to the posterior margin of

the third abdominal segment. Femur of prothoracic leg not visible. Prothoracic tibia and tarsi prominent, reaching down two-thirds the length of the maxillae. Mesothoracic legs extending to the tips of the maxillae. Metathoracic legs invisible. Antennae reaching almost to the tips of the maxillae. Segments 4, 5, and 6 of the abdomen crossed dorsally by a transverse line of tubercles: the surface in front of the ridge coarsely punctate, but the part of the segment caudad of the ridge very finely punctate. On the ventral surface three transverse ridges occurring on segments 5, 6, and 7. Cremaster about as wide as it is long, somewhat flattened dorso-ventrally, very rugose, and bearing four short setae of equal length. Spiracles on the eighth abdominal segment dorsad. Female with two genital orifices. The peculiar sculpturing of the larva carried over and showing somewhat in the pupa.

The adult (Plate XLI, 26)

Length of body of female, 26 mm. Expanse of wings 54 mm. The original description by Walker (1865 : 438) is as follows:

Cinereous brown . . Antennae moderately pectinated in the male, slightly pectinated in the female . . Femora and tibia fringed; spurs moderately long. Fore wings with a dark brown oblique stripe, which extends from the base of the interior border to the tip of the wing, and is very diffuse on the outer side: an oblique fusiform pale cinereous ringlet: another ringlet of like shape and hue, longitudinal, nearer the base, much smaller than the first and often obsolete; two submarginal oblique lines of blackish lunules: exterior border almost straight, rather oblique. Hind wings with a black oblique spot in the disk beneath.

Nonagria oblonga Grote

Nonagria oblonga Grote, a moth which also belongs to the family Noctuidae, has been reported by various authors as boring in the stems of *Typha latifolia*. Walton (1908) has described to some extent the habits of the later larval stages and has figured the full-grown larva, the pupa, and the adult. The writer has found the species to be common on *Typha latifolia* near Lawrence, Kansas, and in the following places around Ithaca, New York: Vanishing Brook, Cascadilla Creek, Bool's Back Water, Renwick Marsh, and Michigan Hollow.

Life history and habits

Nonagria oblonga Grote apparently produces only one generation a year.

Egg-laying.— The writer has been unable to find the eggs of this species, although the work of the larvae, from the first instar on, has been observed for three seasons, two seasons around Ithaca and one season in Kansas. The young larvae may be found just as soon as the cat-tail leaves appear above the surface of the ground. In Kansas, on April 20 1917, when the leaves of the cat-tail were not more than four inches above the surface of the ground, the larvae were found at work in the tips of the leaves.

Although the larvae had evidently just started their work, and more larvae continued to appear during the following days, no eggs could be found on the plants. Again, in Ithaca, on May 20, 1918, first-instar larvae were discovered at work in the tips of the leaves, but no trace of the eggs could be discovered. This suggests the possibility that the females deposit their eggs in the fall on some of the old plants or other objects in the field, and that the species overwinters in the egg stage.

The larva.— The larvae enter the leaf of the cat-tail near the tip and at once begin to work as leaf miners. In their mining they do not restrict their work to the longitudinal channels, as do the larvae of *Arzama obliqua*, but they zigzag back and forth in the leaf, cutting through both the longitudinal and the transverse partitions. They feed on the chlorophyll and on the spongy parenchyma of the plant. The larvae are strictly solitary in their habits; only occasionally do two, or sometimes three, larvae occur in the same mine or even in the same leaf. The characteristic mine produced by the larva is shown in Plate XLII, 37. It is easily distinguished from the mine made by *Arzama obliqua*.

When the larvae are ready for the first molt, they suddenly widen their mine to the outer margins of the leaf, thus producing a narrow transverse mine extending nearly the entire width of the leaf but not severing it completely. This causes the leaf to wither from this point outward to the tip. In this withered part of the leaf the larvae molt, after which they mine downward through the lower, uninjured part. It seems that the natural condition of the leaf, which is very moist, is unfavorable to the molting of these larvae, and it is in order to overcome this excess of moisture that they sever the conducting tissues, thus causing the leaf to dry quickly. In this manner they obtain the required dryness in which to shed their first coat. This allows the larvae to remain under cover, where they are more protected than they would be in the open. The characteristic appearance of such a leaf and the cast skin of one larva in the severed part of the leaf, just above the transverse cut, are shown in Plate XLII, 37.

The larvae of this species do not cease mining after their first molt, and come out of the leaf, as do the larvae of *Arzama obliqua*, but continue as miners in the leaf for some time, often remaining in the leaf through the second, and even through part of the third, instar. Then, however, the larvae crawl away from the upper part of the leaf and seek protection

behind the sheath of the outer leaf, where they feed for a time before they enter the stem and become true stem borers. If the larvae emerge from the leaf soon after the first molt, they usually go down to the sheath of one of the first-formed leaves and there mine in the sheath for some time before entering the stem. Occasionally they feed for a while between two contiguous leaves. The effect of *Nonagria oblonga* Grote is easily recognized on the plant, since the work of the first-instar larva always causes the leaf at first to bend over and wither, and later, after the severed portion has become dry, to break off and fall to the ground. The leaf thus broken at the end, and the presence of the mine, are indicative of the work of these larvae. The writer once found a plant in which five leaves had been cut off by these larvae (Plate XLII, 36).

On entering the stem, the larvae work toward the center, where their borings materially hinder the further growth and development of the plant (Plate XLVII, 70). The presence of the larvae in the stems is indicated by the dried and withered central leaves of the leaf bundle. A plant so affected never heads, because the larva keeps the center tunneled out. The habits of the later larval stages of *N. oblonga* and *Arzama obliqua*, and their effect on the plant, are very similar.

Walton (1908) says of the habits of the larvae: "From all appearances the larva feeds for a time on the sheath of the stem, . . . As it increases in size it bores directly into the succulent central shoot, where it afterward remains until emerging as a mature insect."

When the larvae become full-grown, they transform to the pupal stage in the burrow of the plant. The larva lies with its head upward in the burrow. The exit hole is from two to four inches above the pupa and is carefully plugged up with a combination of frass and plant fibers.

Bird (1902) states that Nonagria has an extremely short pupal stage, from seven to nine days being the record of one brood.

At Ithaca, New York, the writer first found pupae on August 2, 1916. In Kansas the insects mature much earlier. There one larva pupated on June 24, 1917, and emerged on July 5, 1917, the pupal stage covering only eleven days.

The adult.— Around Ithaca the first adults were noticed on August 8, 1916, while in Kansas they were beginning to emerge by the 30th of June. Whether there is a second generation, especially in Kansas where the adults emerge so early, the writer has not been able to ascertain. The

adults failed to mate and lay eggs in captivity. However, no larvae were observed at work on the cat-tails later in the season. Therefore it is likely that if there is a later generation, it occurs on another plant.

Description of the stages

The larva. — The color markings of the larvae (Plate XLVII, 67) vary somewhat in different individuals, but mainly only in the degree of intensity of the colors. They may be described as follows:

General ground color light brown with a slight tinge of flesh color. Head light brown, mottled or speckled with darker brown. Epicranial suture, mandibles, and area just above the clypeus and laterad, darker brown. Six longitudinal, flesh-colored to brownish stripes along the entire length of the body. On each side of the median dorsal line two broad stripes; and laterad to these stripes narrow stripes, located on the lateral margin of the body. Above the spiracles another broad stripe. Below the spiracles, often, another more or less broken line, especially noticeable in the young larvae. Prothoracic shield light brown. At the base of the hairs on the body a dark brown spot. Dorsal surface of the last abdominal segment light brown, speckled with darker spots. Ventral side of the body of a light yellowish color. Length of full-grown larva, from 40 to 50 mm.; width, from 4.5 to 5 mm. Larva cylindrical in shape and not as much flattened as the larva of *Arzama obliqua*.

The pupa (Plates XLII, 33, and XLVII, 71)

Average length 27 mm.; width 7 mm. Color reddish brown, with head, thorax, and cremaster darker brown. Head with a conical projection about 2 mm. long. Wings extending backward over three-fourths of the fourth abdominal segment. Prothorax half as long as the mesothorax. Surfaces of the head and thorax nearly smooth. Anterior margin of labrum sinuate. Labial palpi about two and one-half times as long as the labrum. Maxillae extending about one-sixth of the distance along the fourth abdominal segment. Maxillary palpi present as small triangular pieces. Prothoracic femur visible. Prothoracic legs extending two-thirds the length of the maxillae. Mesothoracic legs reaching a little beyond the tips of the maxillae. Antennae reaching a point half-way between the tips of the mesothoracic legs and the tips of the maxillae. Metathoracic tarsi visible. Abdominal segments 2 to 7, inclusive, dorsally roughened with tubercles, especially prominent on segments 5, 6, and 7. Cremaster somewhat bilobed, with a rough margin bearing four straight setae, two originating underneath, and the other two originating above, laterad to the median line. All these setae equidistant from each other, the middle ones being longer than the outer ones.

The adult. — The adult (Plate XLVII, 68) is of a pale reddish or yellowish color, measuring about 35 millimeters across the extended wings. The original description of the adult, as found in Grote (1882), is as follows:

Male. Pale reddish or yellowish gray, something the color of *Mythimna*, *Pseudaletia*, Guen. Primaries somewhat oblong, internal angle rounded away; apices softened, costa

a little arched. Eyes naked. Clypeus mucronate. Palpi prominent, concolorous. Markings obsolete. The fine dark linear denticulate t. p. line barely discernable. Stigmata very vaguely indicated by paler shades. Hind wings with a faint mesial black shade band; centrally stained blackish; fringe and external edge like abdomen and very little paler than the rest of the insect. Beneath pale, with the disk of fore wings blackish; a common blackish extra-mesial shaded line. Minute black discal points. Smaller than *Typhae*.

Arsilonche albovenosa Goeze

Arsilonche albovenosa Goeze is another member of the family Noctuidae. It is found in Canada and in the northern, eastern, and central parts of the United States. It is a general feeder and has been reported on willow, smartweed, buttonbush, grass, and other plants. *Typha latifolia*, the writer believes, is here reported for the first time as a food plant of this species.

Life history and habits

This moth is reported to have two generations a year. The writer, however, has followed it through only one generation at Ithaca, where two adults emerged on August 15.

Egg-laying.— The eggs are deposited in long patches on the surface of the cat-tail leaf, usually ten to fifteen inches from the tip. The eggs overlap one another as shingles do. They lie on the leaf in rows, the number of rows varying from three to seven, and the rows overlapping one another as well as the individual eggs in each row. The number of eggs in one patch ranges from 60 to 161.

As the egg develops, it becomes much darker, turning very dark just before the larva emerges.

The larva.— Immediately after hatching, the larva devours the empty shell and then begins to feed on the surface of the Typha leaf, where it scrapes off the chlorophyll. As the larva grows and feeds more voraciously, it usually migrates to the end of the leaf, where it eats off the tip of the leaf or devours chunks out of the edge of the leaf, as shown in Plate XLVI, 62.

When the larva has attained its full growth, it ties two cat-tail leaves together, and between them spins a tough cocoon in which it pupates. Two larvae pupated in the laboratory, under the author's observation, on July 23, 1916, and two others on July 25, 1916. The former both emerged on August 15, 1916. This apparently indicates the length of the pupal stage to be nineteen days.

Description of the stages

The egg (Plate XLVI, 61)

Flat; saucer-like or shell-like in shape, and grayish white in color. Diameter, as seen from the top, varying from 0.89 to 1 mm.; thickness of egg about 0.2. Sculpturing very pretty, micropyle in center of dorsal surface consisting of a dot with a rosette of elongate cells around it. Radiating from the rosette to the margin of the egg, about 45 small ridges, indented transversely by small, rounded depressions.

The larva.— The first-instar larva, within twenty-four hours after hatching, is described as follows:

Length 2 mm. Entire head jet black; thoracic shield dark brown; meso- and metathorax light gray with dark tubercles. Segments 1, 4, 5, and 8 of the abdomen dark brown, with gray tubercles. The other segments of the abdomen light yellow, with gray tubercles. From these gray tubercles originate long hairs.

Beutenmüller (1901) gives the following description of the full-grown larva (Plate XLVI, 62):

Head black, with an inverted V mark on the face, two white stripes on top, and mottled with white at the sides. Body black, two yellow lines on each side of the back and one on each side below the spiracles. The body is also mottled with confluent striae, but less so on the dorsum. Warts orange with light and dark bristles; along the extreme sides a row of orange spots. Underside pale whitish. Length 40–45 mm.

The pupa (Plate XLVI, 63)

Length 18 mm., width, 5 mm. General color dark brown. Wings extending as far back as the fourth abdominal segment. Front of the head with two rounded, rugose ridges running up and down. Clypeo-labral suture very distinct. The front margin of the labrum rounded. Labial palpi three times as long as the undivided labium. Maxillae extending down to the beginning of the third abdominal segment. Prothoracic femur visible and the prothoracic tibia and tarsi extending down almost to the tips of the maxillae. Mesothoracic legs extending to the middle of the fourth abdominal segment. Antennae just failing to reach the tips of the mesothoracic legs. Metathoracic tarsi plainly visible. Ventral surface of segments 5, 6, and 7 finely granulate anteriorly, posteriorly finely punctate. The other segments smooth. On the dorsal surface, the metathorax and the first seven abdominal segments very roughly tuberculate. Cremaster broader than it is long and bearing from 40 to 50 short, straight spines.

The adult.— The adult (Plate XLVI, 64) is described as follows by Beutenmüller (1901): "Fore wings white, and more or less heavily marked with fawn brown streaks between the veins, giving the insect a very characteristic appearance. Hind wings and body white. Expanse, 34-45 mm."

Archips obsoletana Walk.

Archips obsoletana Walk. is a moth belonging to the family Tortricidae. This insect has been reported from the Atlantic states and from Illinois. The author has found it in Kansas and in New York. Slingerland (1901) suggested "the obsolete banded strawberry leaf-roller" as a common name for the insect. *Archips obsoletana* Walk., although it lives on various host plants, prefers those which grow in moist situations, and is here reported on *Typha latifolia.*

Life history and habits

The habits of this insect as a leaf-roller on strawberry have been studied rather carefully by Slingerland (1901). According to his report, there are three generations a year in New York. It is not known in what stage the insect passes the winter.

Egg-laying.—The eggs have not been observed in nature. In the laboratory, they were deposited in a large mass on the side of the glass cage.

The larvae.— The writer's observations on the habits of the larvae of this species have been restricted to those specimens found on *Typha latifolia.* The larvae and their work on cat-tail were first noticed on some cat-tail heads from Lawrence, Kansas, sent to the author by Dr. H. B. Hungerford and received at Ithaca on July 17, 1916. A number of the heads showed the effects of the work of the larvae of *Archips obsoletana.* On August 12, 1916, larvae of this species were also found at work on the heads of cat-tail plants in the McLean Bogs. One pupa was also discovered at this time.

The larva works on the immature heads of the cat-tail, feeding on the tender styles of the pistillate flowers and sometimes eating off the tops of the developing ovules (Plate XLVII, 69 and 72). The stigmas are not eaten; instead they are lined underneath with a thin, but closely woven, layer of silk. This silk layer, together with the stigmas on top, forms a protective covering over the larva. When this covering is torn loose, the larva quickly repairs it.

In the laboratory, the larvae at times left the heads and fed on the leaves of the cat-tail; but they always provided themselves with a protected place, either by tying two leaves together or by spinning a silken tube between a leaf and the side of the glass cage. In this tube the larva remained, never leaving it entirely but always keeping the tip of the

abdomen covered and protruding the head to feed. As the larva fed downward, it lengthened this silken tube. In the field, the author has not observed the larvae feeding anywhere on the plant except on the head.

When the larva becomes full-grown, it goes to the top of the head, to which it then ties a leaf in order to form a place in which to spin its cocoon for pupation. The silk used to tie the leaf to the head is covered with a mixture of frass and the remains of the staminate flowers. If a leaf is not within reach of the larva, the cocoon is made on top of the head, near the rachis, and covered with the remains of the staminate flowers. After pupation, the wind and rain soon tear off the covering made by the larva and the head has then the appearance of having been shaved in patches (Plate XLVII, 73).

Description of the stages

The egg.— Slingerland (1901) describes the egg somewhat as follows:

Thin, oval, light lemon yellow, overlapping each other not unlike the shingles of a house. Shell is finely reticulated, the micropyle showing plainly at one end.

The larva.— The larva may be described as follows:

Olive green, with a light brown head and thoracic shield, both marked with black; the body sparsely clothed with light-colored hairs arising from pale, roughened tubercles. The newly hatched caterpillar light yellow, with a brown head. Length of full-grown larva, about 17 mm. (Plate XLVII, 76).

The pupa.— The pupa is shown in Plate XLVII, 74. The following description applies to the female.

Length, including cremaster, 12 mm.; width, measured across the wings, 3.8 mm. General color reddish brown, the wings being somewhat lighter-colored than the rest of the body. Wings reaching back as far as the middle of the fourth abdominal segment. Thoracic region much enlarged, the appendages forming a distinct salient. Front of the head with an inverted Y ridge, as viewed from the cephalic aspect. A transverse ridge at the base of this Y. Clypeus and labrum prominent, and the clypeo-labral suture distinct. Labium clearly visible. Labial palpi one-fourth as long as maxillae. Maxillae extending half way to the tips of the wings. Maxillary palpi elongate and triangular, reaching to the pro-lateral angles of the maxillae. Coxae of mesothoracic legs visible below the maxillae and the femora. Femur and tibia of prothoracic legs large. Mesothoracic legs extending below the tips of the antennae. Antennae shorter than the wings by 0.8 mm. Metathoracic tarsi visible beyond the tips of metathoracic legs and antennae. Genital orifice double. Cremaster slender, tapering, longer than it is broad, and bearing eight stout, curved setae, four extending from the apex and two on each side. Setae of body long and prominent. On the dorsal surface, the first abdominal segment smooth. Segments 2 to 8, inclusive, each having two

transverse rows of strong spines, most prominent on segments 4, 5, 6, and 7. A few spines present on the ninth abdominal segment.

The adult. The following description of the adult (Plate XLVII, 75) is quoted from Slingerland (1901):

General color varies from a wood-brown through cinnamon to russet; the hind wings and all four wings beneath are of a lighter yellowish-brown color. Many fine, wavy, transverse, dark brown lines occur on the front wings, showing more distinctly in the male. And extending obliquely across these wings is a broad, dark brown band, more or less obsolete in the middle, and there is a subapical spot of the same color on each front wing.

Lymnaecia phragmitella Staint.

Lymnaecia phragmitella Staint. is a little moth belonging to the family Tineidae. Without question, this is the most common and the most abundant of the insects infesting the cat-tail. In distribution it is world-wide. It is found in England, central and southern Europe, northern Africa, Australia, New Zealand, and the United States. Its host plants are *Typha latifolia* and *T. angustifolia*. The writer has invariably found that the majority of Typha plants in any patch are infested by this insect.

Life history and habits

The larva.— Regarding the larvae of this species, Stainton (1870) wrote:

If we visit a boggy piece of ground where *Typha latifolia* grows, we shall find that some of the thick club-like heads of that plant exhibit a curious, tattered and frayed appearance; if the period of our observation be autumn, we shall find on examining amongst the soft downy interior of the fertile catkin some small larvae; if we seek at the end of winter or in early spring, we shall find the same larvae, nearly full fed, about five lines long; and if these larvae are rather broad and flat, of a yellowish-white, with broad darker lines, we need not hesitate to pronounce them the larvae of *Laverna phragmitella.*

The larvae restrict their work to the head of the plant, except occasionally when they bore into the stem to transform (Plate XLII, 35). The young larvae feed on the tender styles of the pistillate flowers, but as these grow larger and become dry, the larvae move farther inward and eat the seeds of the plant. As cold weather approaches, they migrate still farther inward, and finally locate near the rachis of the flower spike, where they often eat away the basal part of the little stalks which bear the seeds. The larvae spin an abundance of silk with which they tie the down, or pappus, together, thus keeping it from being torn off or blown away.

The cat-tail heads which are infested by these larvae present a striking appearance. The silk spun by the larvae holds the downy material together and does not allow the seeds to escape, but the heads fluff out

greatly and become twice or three times their natural diameter. Two heads, one heavily infested with the larvae of *L. phragmitella*, and the other uninfested, are shown in Plate XLV, 59. This is the appearance of the heads in the fall. During the winter and spring the uninfested heads lose all their seeds so that only the rachis remains, but the infested heads retain their seeds in the fluffy condition just described till the following summer, when the heads finally drop to the ground. A field in which the majority of the heads are heavily infested is shown in Plate XLIX, 84. This photograph was taken in July, just about the time that the new heads were forming. In the old heads, as well as in the newly formed ones, these larvae were present.

The larvae overwinter in the half-grown stage in the head of the plant, the fluffy material of the fruiting spike being their protection.

In the latter part of May or early June the larvae attain their full growth. Then, in the midst of the downy material, the larvae spin their thin, tough, white cocoons and transform to the pupal stage. Many of the larvae, leaving the heads, go down and bore into the stem of the cat-tail plant, forming burrows which they line with silk; and there they pupate.

In the laboratory, larvae were placed in vials containing little bunches of seeds from the head of Typha. The larvae spun cocoons in the vials and pupated. Some of the larvae bored into the corks, lined the tunnels with a little silk, and then transformed.

The average pupal stage lasts 29.4 days. This was ascertained from data on five individuals in the laboratory, as shown in table 7. Cocoons

TABLE 7. DETERMINATION OF THE PUPATION PERIOD OF LYMNAECIA PHRAGMITELLA STAIN.

Specimen	Date of pupation	Date of emergence	Length of pupal period (days)
1	June 4	July 1	27
2	June 6	.....	..
3	May 30	July 1	32
4	May 31	July 3	33
5	June 5	July 6	31
6	June 4	June 28	24
Average	....	.....	29.4

and pupae, as they were removed from the pappus of the head of a Typha plant, are shown in Plate XLVIII, 82.

The adult.— The first adults were observed to emerge in the laboratory on June 8, 1916, and the maximum emergence occurred between June 25 and June 30. In the spring of 1918, the moths first appeared in the laboratory on June 10. Immediately after emergence the adult moths often rest on the cat-tail heads, as shown in Plate XLIX, 85. Stainton (1870) speaks of the adult as follows:

> If in July we visit a locality in which the *Typha latifolia* grows we may probably find towards evening some small grayish-ochreous moths, with the anterior wings rather streaked with brownish towards the apex, and with two dark brown spots ringed with white on the disc; these would no doubt be the perfect insects of *Laverna Phragmitella.*

Description of the stages

The larva (Plate XLII, 32)

Length from 10 to 12 mm., width 2.5 mm. General ground color yellowish white. Ventral side entirely white, with the exception of the brownish, chitinized legs and prolegs. Dorsal surface with 5 longitudinal brown stripes. The median stripe rather narrow; the next stripe, on each side of the median line, wide and somewhat lighter in color; the stripes on the lateral margin, above the spiracles, more or less broken into blotches. Head light yellow, blotched with brown. Epicranial suture dark brown. Posterior part of the head dark brown. Mandibles and labrum dark. Prothorax mottled with dark brown. The last abdominal segment dotted with dark brown spots, as shown in Plate XLII, 32.

The pupa (Plate XLII, 34)

Length 9–10 mm., width 2.1–2.3 mm. General color yellowish brown. Head with a blunt, rounded projection. Wings reaching to the middle of the sixth abdominal segment. Front of clypeal suture faint. Labrum with outer margin rounded. Labium not visible. Maxillae broad at the base and much narrower at the proximal half. Maxillary palpi present as small triangular pieces. Prothoracic legs extending two-thirds the length of the maxillae. Mesothoracic legs not reaching quite to the tips of the maxillae. Antennae very slender, reaching the tips of the wings, and contiguous all the way to the tip. Metathoracic legs invisible. Rudimentary prolegs visible on the sixth segment. No definite sculpturing on the body. On the dorso-caudad surface of the last abdominal segment, eight hooked setae, arranged in groups of four. In each group three setae in a straight transverse line, but the fourth seta just cephalad to the middle one of the group. Cremaster undeveloped.

The adult.— The length of the adult, with wings folded, is from 10 to 12 mm. Stainton (1870) gives the following description of the adult:

> Head pale brownish-ochreous, face paler. . . Antennae pale grayish-ochreous, spotted with dark fuscous. . . Anterior wings pale brownish-ochreous, the costa beyond the

middle paler: on the disc, nearly in the middle, is an elongate dark brown spot surrounded by white, and in a line with it at the end of the discoidal cell is another similar spot a brownish streak frequently connects the two, and the entire apical portion of the wing is more or less streaked with brown. . . Posterior wings pale gray, with grayish-ochreous cilia.

Dicymolomia julianalis Walk.

Dicymolomia julianalis Walk. is a member of the family Pyralidae. It is found throughout the southern part of the United States. Ithaca is probably near its northern limit. Its host plant is *Typha latifolia*.

Life history and habits

Dicymolomia julianalis Walk. has but one generation a year. It passes the winter in the half-grown larval stage. The habits of this insect are very similar to those of *Lymnaecia phragmitella*.

Egg-laying.— The eggs of *D. julianalis* are placed in the heads of the cat-tail, being inserted singly in the down, or pappus, of the seed. They are fastened to the pappus at about the level of the kernel of the seed. The eggs were first found on July 25, 1918, at which time they were rather common. It was not at all difficult to locate them, once it had been discovered where to look for them. The period of egg-laying has not been carefully determined, but apparently there were no eggs laid before the middle of July and none after August 10. The eggs are placed in the heads of the cat-tail with the blunt, or anterior, end outward. Several eggs are shown in the cross section of a head of *Typha latifolia*, in Plate XLIII, 45.

On July 25, 1916, the writer watched one of these eggs hatch. The larva lay in the egg, stretched to its full length, and could be seen moving back and forth inside the egg shell. It ate its way through the egg shell and escaped (Plate XLIII, 46). When about half of its body was out of the shell, the larva gained a foothold on the pappus and pulled itself the rest of the way out of the shell. The larva does not devour the empty shell, but at once buries itself in the head of the plant, where it eats the tender styles of the pistillate flowers. The empty shell remains attached to the pappus. The time from the moment that the larva actually began to eat through the egg-shell till it was freed was about twenty-five minutes.

The larva.— *D. julianalis* spends its entire larval period in the head of the cat-tail, obtaining its food, first from the styles of the pistillate

flowers, and later from the seeds and the dried-up parts of the flower. As soon as hatched, the larva begins to feed on the styles, leaving the stigmas to form a sort of covering over itself. These severed stigmas are spun together with a little silk and thus held in place. The larval habits of both *Lymnaecia phragmitella* and *D. julianalis* are very similar in their early stages. As the cat-tail heads become more mature, and the larvae grow larger, they enter deeper into the head, and their presence is not so readily detected as when they are working near the outer surface where the little raised patches of fluffy material they produce are easily seen. The appearance of a head of Typha within a week after the larvae had hatched and entered the head is shown in Plate XLIX, 86. As in the case of *Lymnaecia phragmitella*, the seeds are kept from scattering, by being tied together with silk woven by the larva. Neither wind nor rain is able to tear apart the heads so protected. Accordingly they form a good shelter for the larvae during the winter. The larvae of *D. julianalis* bore into the axis of the flower spike and there spend the winter in the half or two-thirds-grown stage. The rachis, with the characteristic tunneling of the larvae, is shown in Plate XLIII, 42 and 43. These tunnels are later lined with a little silk and in them the larvae construct tightly-woven cocoons in which they transform to the pupal stage. Many of the larvae, however, remain in the fluffy material in the heads to spin their cocoons and pupate. Pupation begins about the first of June. The adults emerge during the latter part of June and the first part of July.

During the spring of 1916 the author did not find any dead larvae in the heads of the cat-tail; but in the spring of 1918 all the larvae of this species which he observed were dead, evidently having been killed by the severe cold of that winter. At that time even the larvae in tunnels of the axes of the heads were dead. This was not true of the larvae of *Lymnaecia phragmitella*, however.

Description of the stages

The egg

Elongate oval, tapering considerably toward the posterior end and rather blunt at the anterior end (Plate XLIII, 38). Very long in proportion to its width, measuring 1 mm. in length and 0.219 mm. at its greatest diameter. Color of egg white, with a slight bluish tinge in refracted light. Sculpturing rather faint, consisting of fine, more or less hexagonal reticulations (Plate XLIII, 39, drawn with the camera lucida).

The larva.— The larva of the first instar is shown in Plate XLIII, 40. The following description is taken from a larva about thirty minutes after its emergence from the egg:

Length 1.19 mm., greatest width 0.28 mm. General color light pinkish or flesh color. Head and thoracic shield mottled with darker brown, restricted in the thoracic shield to the posterior part. A dark mottled area on the dorsal surface of the last abdominal segment also.

The full-grown larva (Plate XLIII, 41) is described thus:

Length from 7 to 10 mm.; about 2 mm. at its greatest width. Much flattened, and in general shape much like *Lymnaecia phragmitella*. General color flesh color. No special markings on the body except, as in the first instar, on the dorsal surface of the first thoracic segment and on the last abdominal segment. Head dark brown, with darker blotches near the outer margin. Epicranial suture very dark brown. Prothoracic shield dark brown, slightly lighter than the head, with two oblique oval spots near the lateral margin, the shield being mottled near the posterior margin. Dorsal surface of the last abdominal segment mottled with brownish patches or spots, as shown in Plate XLIII, 41. Larva easily distinguished from that of *Lymnaecia phragmitella* in that it does not possess the five longitudinal stripes on the dorsal surface of the body.

The pupa (Plate XLIII, 44)

Length 7–8 mm., width 2.9–3 mm. General color yellowish brown to dark brown. Front of head not visible from the ventral aspect. Clypeo-labral suture distinct. Labrum with an emargination and very small, appearing somewhat like an arrow head. Two long hairs on the clypeus. Wings extending two-thirds across the fourth abdominal segment. Maxillae extending to the wing tips. Maxillary palpi absent. Prothoracic femora visible. Prothoracic leg extending two-thirds the length of the maxillae. Mesothoracic legs reaching to the tips of the wings. Antennae reaching to a point halfway between the tip of the prothoracic leg and the tips of the maxillae. Metathoracic legs not visible. Cremaster subquadrate, nearly smooth, with six equally long, hooked spines arranged in groups of threes on the outer angle of the cremaster. Rudiments of prolegs on segments 5 and 6 of the abdomen. General surface of the body smooth.

The adult.— The adult female, shown in Plate XLVIII, 81, measures 6 mm. in length and has a wing expanse of 18 mm. Walker (1859) describes the adult as follows:

Whitish, slightly marked with ferruginous. . . Antennae stout, submoniliform. Abdomen with brownish speckles. . . Legs stout. . . Fore wings with two reddish bands: the first exterior; the second marginal; the intermediate part with blackish speckles, which are somewhat confluent by the bands.

COLEOPTERA

Calendra pertinax Oliv.[4]

Calendra pertinax Oliv. is a beetle belonging to the family Calandridae. Blatchley and Leng (1916) state that *Calendra pertinax* "ranges from New England and Canada to Michigan and Utah, south to Florida." Satterthwait (1920) reports this species from the following states: Indiana, Missouri, Maryland, and New York. The author has collected and reared it in Lawrence, Kansas, and in Ithaca, New York. A variety of *pertinax*, called *typhae* Chittendon, has been reared from the roots of *Typha latifolia* in California. The known host plants of *C. pertinax* are *Typha latifolia*, *Acorus calamus*, corn (*Zea mays*), and *Sparganium* sp. The writer has found *C. pertinax* in *Typha latifolia* and in *Sparganium* sp.

Life history and habits

The weevil is found to be most abundant in Typha patches where the plants grow in sod or grassy soil. This has been found to be true in New York as well as in Kansas. In the wet, grassy places along the railroad tracks south of Ithaca, where Typha grows intermingled with various species of grasses, the larvae were found to be most numerous. In some of these patches nearly every plant was infested. However, the weevil was found also in the larger cat-tail patches of Renwick Marsh around the biological field station.

Egg-laying.— The eggs are inserted into the outer sheath at the base of the plant, very near the surface of the ground. No females were actually observed in the act of ovipositing, but the newly laid eggs were always found with the end protruding from a little slit in the sheath (Plate XL, 17). In very wet places it is likely that the eggs are placed above the surface of the water, but the writer observed them only on cat-tails growing in a rather dry situation.

The period of egg-laying has not been fully determined. Eggs were first found in Kansas on June 28, 1917. At that time, however, first- and second-instar larvae also were found in the plants, so that egg-laying must have started some time before, probably as early as the latter part of May. Eggs were found in the stems as late as July 17, when the

[4] Determined by Dr. E. C. Van Dyke.

observations had to be discontinued. The period of egg-laying is therefore spread over a number of weeks.

The larva. — In the laboratory, the larvae were placed in tin salve boxes which had been partly filled with sterilized sand and moistened with boiled water. A little excavation was made at one end of a fresh piece of the rhizome of cat-tail, and in this the larva was placed and left to feed. Such pieces of rhizome, two or three inches long, remained fresh from three to five days. As the larva became older and needed more food, these pieces of rhizome had to be replaced more often. By splitting the piece open, excavating a little hole in the center for the larva, and then binding the pieces together again with rubber bands, observations could be made from day to day without unduly disturbing the larva.

As soon as the larvae are hatched, they begin to bore directly into the stem, working toward the center, and thence downward toward the crown, and from there into the central axis of the rhizome (Plate XL, 19). Like the other borers of the cat-tail, this larva at once seeks the central part of the plant, where the tissue is most tender and succulent. However, the weevils seem to have a special preference for starchy food, and for this reason they work downward to the rhizome, the core of which is composed mainly of starch (Plate XLV, 60). In rearing the larvae, it was found that they would not eat any other part of the rhizome except the starchy core. As many as seven larvae have been found in a single plant. In one instance they were all working at the crown and as a result had nearly cut off the plant.

The affected plants present a somewhat stunted appearance. Sometimes the central leaves die and the plant fails to head out. The tunneled rhizomes shrivel up considerably and often darken decidedly.

The larvae grow very rapidly, and the time from hatching to the pupal stage averages about three weeks. When the larva has become fully grown, it prepares an oblong pupal cell in the stalk of the plant, from one to three inches above the ground (Plate XLVIII, 80). The pupal cell is made of partly masticated pieces of the stalk, with which the burrow is plugged above and below. In the laboratory some of the larvae pupated in their burrows in the rhizome, while others, that were reared in plants growing in flower pots, tunneled through the soil to the bottom of the pot and there made a smooth, oblong, unlined, earthen cell in which they transformed. The reason for their going down into the soil appeared to be a

desire for a moist place in which to pupate. The plants in the pots had dried up completely, and the soil, too, was quite dry, so that in order to find a moist place the larvae were forced to go to the bottom of the pot.

The length of the pupal stage seems to vary considerably. Eight pupae were kept under observation, and the results are given in table 8:

TABLE 8. LENGTH OF PUPAL STAGE OF CALENDRA PERTINAX OLIV.*

Specimen	Date of pupation	Date of emergence	Length of stage (days)
1	July 15, 1917	July 24, 1917	9
2	July 15, 1917	July 22, 1917	7
3	July 19, 1917	.....	Died
4	July 21, 1917	July 27, 1917	6
5	July 27, 1917	.....	Put in preservative
6	July 26, 1917	August 8, 1917	13
7	July 29, 1917	August 11, 1917	13
8	July 29, 1917	August 11, 1917	13
Average			10.16

* The data on the first six pupae were determined for the writer by Dr. P. B. Lawson, of Lawrence, Kansas. The last two pupae were observed by the author himself.

Description of the stages

The egg (Plate XL, 16)

Average length 2.15 mm., average greatest width 0.85 mm. Elongate oval, scarcely subreniform-elliptical. Color almost pure white. No distinct marking or sculpturing. As the time of hatching approaches, turning yellowish, and becoming quite dark just before the larva emerges.

The larva (Plate XLVIII, 77)

Color dirty white. Head yellowish brown. Epicranial suture distinct. On each side of the epicranial suture a light line starting indistinctly at the vertex and running obliquely to the frontal suture. Mandibles very dark brown, almost black. Front of head darker near the fronto-clypeal suture. Clypeus light brown. Labrum with two curving sulci which divide it into three subequal parts. On the labrum four prominent hairs and a number of marginal hairs. Thoracic segment distinct. Prothorax with a yellowish, chitinized shield. Spiracles of prothorax large, oblong, and nearly twice as large as the other spiracles. Segments 4, 5, and 6 of the abdomen greatly enlarged. Spiracles located on the dorsal surface. Length of larva, in its curled-up position, about 13 mm.; when straightened out, about 16–17 mm.; greatest diameter 7 mm.

The pupa.— The pupa is shown in Plate XLVIII, 79. The size of the pupae varies considerably. The average of the measurements of six pupae (table 9) showed the average length to be 14.2 millimeters and the width, taken across the prothorax, 5.76 millimeters.

TABLE 9. MEASUREMENTS OF THE PUPA OF CALENDRA PERTINAX OLIV.

Specimen	Length (millimeters)	Width (millimeters)
1	15 8	7.0
2	13 2	5.2
3	12 5	4.8
4	15 4	6.3
5	14 8	5.8
6	13 5	5.5
Average	14 2	5.76

The pupa is large, naked, and dirty white in color. It may be described as follows:

From the dorsal view: Head almost or entirely concealed by the prothorax. Prothorax a little longer than the meso- and metathorax combined. Eight spines on the surface of the prothorax, arranged in pairs, near the four corners of the subrectangular dorsum. Mesothorax terminating in a triangular lobe, without spines or setae. Metathorax with two prominent setae. On each of first six abdominal segments a transverse row of setae arranged as follows: segment 1, with a group of three setae on each side of the median line and one laterally just above the spiracle; segments 2 to 6, inclusive, with the same arrangement except that the groups laterad of the median line have four setae; segment 7 with one seta on the lateral margin; segment 8 with stout spines, arranged in groups of fours, on the posterior margin.

From the ventral view: Rostrum stout, reaching to the prothoracic tarsi. One pair of spines at the base of rostrum and another pair in line with the base of the antennae. Antennae elbowed and reaching almost to the tips of the femora. Each femur with a stout spine near the distal end. Wings reaching to the ends of the hind femora. On the eight abdominal segments, in each of the outer two apices, eight spines, arranged in groups of fours.

The adult.— Blatchley and Leng (1916) describe the adult (Plate XLVIII, 78) as follows:

Elongate-oval. Black or reddish-black, shining, the interspaces of thorax and flat alternate intervals of elytra covered with a dirty white coating. Beak as in key, three fourths the length of the thorax, finely and sparsely punctate, foveate and finely grooved above at base. Thorax longer than wide, foveate and finely constricted; vittae entire, the median one widest at middle, narrowed before and behind; lateral ones with edges sinuous, branched as described

above; interspaces and sides of disc coarsely punctate. Elytra broadest at humeri, sides feebly converging to apical fourth, then more strongly to the rounded apex; striae with rather coarse, regular punctures; the broader and more convex intervals somewhat interrupted, minutely and sparsely punctate. Length 11–15 mm.

Notaris puncticollis Lec.[5]

According to Blatchley and Leng (1916), *Notaris puncticollis* Lec. (Plate XLVIII, 83) ranges from Newfoundland and Quebec to Minnesota and as far south as the Ohio River. The host plants reported for this species are cabbage, *Peltandra virginica*, and *Typha latifolia*. Webster (1893), writing of *Notaris puncticollis*, says:

> In Wayne County, Ohio, a field of this swamp land was underdrained last year, and last January was plowed; no further cultivation being given it until late spring, when it was prepared and planted to cabbage, about 50,000 in number, set late in June. These have been attacked and many of them destroyed by the adults of two species of Rhynchophora (*Listronotus appendiculatus* Boh. and *Erycus puncticollis* Lec.). The former is supposed to be the chief depredator, though I myself saw the latter attacking the plants. First, great cavities are gouged out of the stems of the young plants, and later the base of the larger leaves are attacked from beneath. . . . . It is not unlikely that one and perhaps both of these species breed in Sagittaria, though I have some reasons for suspecting that the Erycus may breed in the common *Typha latifolia* or cat-tail.

On August 19, 1915, at the field station in Renwick Marsh, W. A. Hoffman found the adult of *Notaris puncticollis* Lec. in the burrow in the stem of Typha. The burrow appeared very much the same as that of *Calendra pertinax*. The writer, however, has not been able to find this species during the course of his studies.

HEMIPTERA

Ischnorrhynchus resedae Panz.[6]

Ischnorrhynchus resedae Panz. is an insect belonging to the family Lygaeidae. It is of general distribution, being reported from Europe, Asia, Central America, Mexico, Canada, and the United States. Among its host plants are included birch, conifer, heath, arbutus, *Typha latifolia*, and *T. angustifolia*. The two species of Typha are here reported for the first time.

Life history and habits

Egg-laying.— The eggs are laid in the spring, during May and June. They are deposited singly in the pappus of the old cat-tail heads of the

[5] Determined by C. W. Leng.
[6] Determined by Dr. H. H. Knight.

previous year. They are attached either to the seeds or to the pappus. When the egg hatches, the nymph either opens the cap or breaks through the egg shell, bursting it near the top.

The nymphs.— The various nymphal stages and the adults were first observed on the overwintering cat-tail heads in the summer of 1916. It was at first assumed that they were merely accidentally present on the cat-tail heads, but closer examination revealed that the bugs were feeding on the dry seeds of the heads.

The nymphs obtain their nourishment by thrusting the stylets of their beaks into the dry seeds (Plate XLIV, 53 and 55). During feeding, the long labium is often folded back under the body. In just what manner the bugs are able to extract nourishment from the dry seeds the author has not been able to determine. When crushed on the slide and examined under the microscope, the seeds show very little moisture. It is very probable that the insects secrete a fluid which dissolves or predigests the dry food material before it is taken into the body. The author has succeeded in rearing nymphs to the adult stage on these dry heads of cat-tail alone with no other food available. When placed on the green leaves of the cat-tail, the nymphs insert their beaks and feed. They are easily disturbed while feeding on the seeds in the laboratory. At the slightest provocation they rise up on their hind legs, quickly extract their stylets, and, by means of their front legs, stroke the stylets back into the labium. The labium is then folded into place and the nymph retreats to some sheltered place.

The adult.— Adults were found mating in May and June. The female inserts her ovipositor into the male and copulation lasts from six to nine minutes. Mating is repeated a number of times at intervals of from five to ten minutes.

Description of the stages

The egg (Plate XLIV, 47)

Length 0.93 mm. to 1 mm., greatest diameter 0.29–0.30 mm. Egg elongate oval in shape, tapering considerably at the posterior end, and closed by a cap at the anterior end. This cap with a cone-shaped protuberance in the center and surrounded by a circle of hooked spines. The upper two-fifths of the egg finely reticulated; the lower three-fifths with longitudinal wavy and branching ridges. Color lemon yellow at first, turning bright red before the nymph emerges. Empty egg shell white. The egg closely resembling the seed of cat-tail, both possessing caps and very similar markings on the surface.

The first-stage nymph (Plate XLIV, 48)

Length 0.857 mm.; greatest width, across wing pads, 0.280 mm. Length of antenna 0.428 mm. When first emerging from the egg, the general color of the nymph bright red. Eyes carmine red. Abdomen, vertex of head, and lateral margins of the body, of a darker color than the rest of the body. Thorax, front of head, antennae, and legs, of a light yellowish color. Several hours after hatching, nymph of a different appearance: Head, thorax, and tip of the abdomen very dark red, almost brown. Abdomen carmine, mottled with yellow. Legs and antennae greenish yellow, the antennae lighter at the joints. The epicranial suture and the median dorsal thoracic line lighter in color.

The second-stage nymph (Plate XLIV, 51)

Length 1.5 mm.; greatest width, across wing pads, 0.368 mm. Length of antenna 0.575 mm. General color carmine red. Head and thorax dark reddish brown. Intermixed with the red color of the abdomen, many yellowish blotches. Antennae dark red, lighter at the joints. Rostrum somewhat lighter than the rest of the head. Epicranial suture and median thoracic line pale. First thoracic segment uniformly dark; in the second segment the dark color restricted to two rectangular patches; in the third segment the darker color present in two transverse lines. The dorsal glands showing as short, brown, transverse lines between the abdominal segments 3 and 4, 4 and 5, and 5 and 6.

The third-stage nymph (Plate XLIV, 50)

Length 2.08 mm.; greatest width, across wing pads, 0.598 mm. Length of antennae 0.69 mm. General color a little darker than in the preceding stage. Head uniformly dark brown, except for the lighter epicranial suture and a lighter spot on the rostrum. Head and thorax covered with faint white pile. In this stage the pro- and mesothorax uniformly dark brown, with the dark patches on the metathorax a little wider than in the preceding stage. The light median line on the thorax present as in the previous stages. The mottled appearance of the red and yellow color of the abdomen more pronounced in this stage. Dorsal glands more plainly visible. Wing pads just beginning to show. Entire body more hairy than in preceding stages.

The fourth-stage nymph (Plate XLIV, 49)

Length 2.71 mm.; greatest width, across wing pads, 0.989 mm. Length of antennae 1.04 mm. Color of head and thorax dark brown. Epicranial suture and median dorsal line of thorax light red. Rostrum of head with a short black longitudinal line on each side. Eyes carmine red. Antennae slightly lighter than head and thorax, much lighter at the joints. Dorsum of prothorax on each side with a blackish, triangular, transverse spot, as shown in Plate XLIV, 49. Wing pads extending 5 mm. beyond the posterior margin of the mesothorax. The mottled color of the abdomen much as in the preceding stage. The white pile on the head and thorax thicker and more plainly visible than in preceding stages. Dorsal glands as in third stage.

The fifth-stage nymph (Plate XLIV, 54)

Length 3.35 mm.; greatest width, across wing pads, 1.61 mm. Length of antenna 1.38 mm. The general color similar to that of the previous stage, but the head and thorax now distinctly patterned. Epicranial suture as in previous stages. The part of the head back of the epicranial suture uniformly dark red. Rostrum yellowish with brown lines on each side, which meet behind the rostrum and then diverge outward until they join the brownish border inside the epicranial suture, thus producing on the head four yellowish patches separated by the brown lines in the shape of the letter X. Prothorax dark brown, punctate with circular yellow spots. From these spots, short white hairs arising. Transverse dark bands on the prothorax, as indicated in Plate XLIV, 54. Rest of thorax, including wing pads, dark brown. The surfaces of meso- and metathorax and the wing pads punctate with yellowish spots, less numerous than those on the prothorax, however. The bases of the wing pads indicated by light-colored, diagonal lines. The margin of the entire thorax and wng pads of a blackish brown color. Wing pads reaching to about the middle of the third abdominal segment. Abdomen colored much as in the preceding stage.

The adult (Plate XLIV, 52)

Female, length 5.4 mm.; greatest width, across the prothorax, 1.5 to 1.6 mm. Length of antenna 1.75 to 1.85 mm. General color dark brownish red. Posterior margin of head and area around eyes and ocelli black. Sides of rostrum black. Basal segment of antennae black, second and third segments of antennae yellowish brown with fuscous at the bases and apices, and the fourth segment dark red. Head and thorax thickly covered with dark punctures. Pronotum with two wavy transverse dark bands near the anterior margin. Corium pale yellowish brown with two black spots on the disk and four black spots on the inner lower margin. Legs reddish brown. Apical segments of tarsi black. Body covered with a very fine white pile. Male slightly smaller than female.

Siphocoryne nymphaeae Linn.[7]

Siphocoryne nymphaeae Linn., the reddish brown plum aphis, is found in numbers on cat-tail during the spring and summer. This species also uses other water plants as its summer hosts, such as Nymphaea, Potamogeton, and others. The aphids are found on the surfaces of the leaves from the sheath out to the tip of the leaf. The writer observed this species on *Typha latifolia* at Ithaca in 1915, 1916, and 1918.

Aphis avenae Fab.[8]

The author found *Aphis avenae* Fab., the oat aphis, in large numbers, feeding on cat-tail, during the spring and summer of 1917, at Lawrence,

[7] Determined by Dr. Edith M. Patch.
[8] Determined by J. J. Davis.

Kansas. Frequently the young aphids were found behind the sheaths of the leaves, in the gelatinous material below the surface of the water in which the plants were growing.

Rhopalosiphum dianthi Schrank

Rhopalosiphum dianthi Schrank was reported on cat-tail by Sanborn (1906).

Rhopalosiphum persicae Sulz.

Rhopalosiphum persicae Sul. was reported on *Typha latifolia* and on *T. angustifolia* by Wilson and Vickery (1918).

Aphis gossypii Glov.

Aphis gossypii Glov. is found in small numbers on *Typha latifolia* during the spring and fall, according to Davidson (1917:65).

Macrosiphum granarium Kirby

Macrosiphum granarium Kirby, the grain aphis, is found in great numbers on Typha during the summer and fall, according to Davidson (1917:65).

Hyalopterus arundinis Fab.

Hyalopterus arundinis Fab., according to Davidson (1917:65), is found from April to June. The infestation on cat-tail is never large. There are four to ten generations. Aphids settle mainly on both sides of the blades, locating in colonies, usually not far from the tips.

HYMENOPTERA[9]

Five species of parasitic Hymenoptera were reared on insects which were found on cat-tails.

Aleiodes intermedius Cress

Aleiodes intermedius Cress was reared on larvae of *Arsilonche albovenosa*. On August 12, 1916, six specimens emerged from one larva.

[9] Determined by C. F. W. Muesebeck.

Apantales cinctiformis Vier.

Apantales cinctiformis Vier. was reared on larvae of *Nonagria oblonga*. A number of specimens emerged on August 8, 1916.

Elachertinae sp.

Five specimens of *Elachertinae* sp. were reared from a larva of *Lymnaecia phragmitella*. These emerged on June 15, 1916.

Pimpla indagatrix Walsh

On June 8, 1916, several specimens of *Pimpla indagatrix* Walsh emerged from the heads of cat-tails which had been kept in a covered jar in the laboratory.

Pimpla inquisitoriella D. T.

Several specimens of *Pimpla inquisitoriella* D. T. were reared from pupae of *Arsilonche albovenosa*.

DIPTERA[10]

The following flies were reared from cat-tail.

Platychirus quadratus Say

Platychirus quadratus Say was reared from the heads of cat-tail. The larvae were noticed in early spring in the overwintering cat-tail heads. Many adults emerged between May 21 and June 10.

Macrosargus clavis Will.

The larvae of *Macrosargus clavis* Will. live in the burrows made by the larvae of *Arzama obliqua* Walk. or of *Nonagria oblonga* Grote. They winter over in the larval stage, and the adults emerge in May and in early June.

Chaetopsis aeneae Wied.

The larvae of *Chaetopsis aeneae* Wied. also are found in the burrows of *Arzama obliqua* Walk. and of *Nonagria oblonga* Grote. Adults emerged on August 8.

[10] The first three species were determined by Dr. O. A. Johannsen, the last one by Dr. J. D. Tothill.

Sturmia nigrita Town.

Sturmia nigrita Town. is a parasite which was found living in the larva of *Arzama obliqua* Walk. In each of the two instances observed, there was only one parasitic larva present in each of the larvae of *Arzama obliqua*. Both dipterous larvae emerged from their host on March 25, 1918, through an opening which was made on the ventral side of the first thoracic segment. They pupated on the following day, and one adult emerged on April 9 and the other on April 10.

RÉSUMÉ

From an ecological point of view, the insect inhabitants of Typha may best be considered with respect to the part of the plant they affect. Accordingly they are thus classified in the following pages.

INSECT INHABITANTS OF THE HEAD OF TYPHA

The insects inhabiting the head of Typha include, among the Lepidoptera, *Lymnaecia phragmitella* Staint., *Dicymolomia julianalis* Walk., *Archips obsoletana* Walk.; and among the Hemiptera, *Ischnorrhynchus resedae* Panz.

The work of *L. phragmitella* and *D. julianalis* is very similar. Each has one generation a year. Their early larval habits are almost identical. They feed first on the tender styles of the pistillate flowers of the cat-tail plant, leaving the stigmas to form a covering over themselves. Later, they advance deeper into the head and feed on the seeds and other parts of the fruiting spike. Both overwinter in the half-grown larval stage. In the spring before pupation, however, their habits become somewhat different. Many of the larvae of *D. julianalis* bore into the rachis of the head, where they transform. The majority of the larvae of *L. phragmitella*, on the contrary, remain in the pappus of the cat-tail, where they pupate in closely woven cocoons. A few of the *L. phragmitella* larvae migrate down to the stalk of the plant, where they bore into the stems and transform. The adults of both species emerge at about the same time.

L. phragmitella is a species of world-wide distribution, while *D. julianalis* is generally restricted to the Southern States, though it is found as far north as New York. Of *L. phragmitella* the writer has found as many as 76 pupae in a single head, while of *D. julianalis* he has never observed more than six or eight individuals in one head.

Both of these insects are well adapted to live in the heads of cat-tail. Both spin an abundance of silk whereby they tie the pappus together and keep the head from being torn and the seeds from being scattered. This process of tying the pappus together assures the larvae of retaining their food supply and also furnishes them a protected and sheltered place for passing the winter. *D. julianalis*, however, being a less hardy southern form, was unable to stand the severe temperature during the winter of 1917 18, and all the larvae found in the Typha heads that spring were dead.

Archips obsoletana should probably be classified as an incidental feeder on cat-tail. It is a typical leaf-roller, occurring chiefly on strawberry plants. However, once the larvae locate on the head of the cat-tail, they spend the entire larval period there and transform to the pupal stage on the plant. Since there are three generations a year, it is very probable that never more than one generation is passed on cat-tail; for these insects feed only on the tender styles of the pistillate flowers, and as these soon dry up, the later generations would not be able to find the tender food they relish. When living on the strawberry plant, these larvae roll themselves up in a leaf for protection. On the head of cat-tails they protect themselves by tying the stigmas together underneath with a lining of silk, thus forming a cover under which they live while feeding on the styles of the flowers. When placed in a cage with cat-tail leaves, the larvae prepare a covering for themselves by tying two leaves together and crawling between them. At the time of pupation they tie a leaf to the head of the plant and thus obtain the protection necessary during their transformation.

In the spring, the females of *Ischnorrhynchus resedae* deposit their eggs in the old, downy heads of the cat-tail. The eggs closely resemble the seeds of cat-tail and thus are well protected from enemies. Immediately after hatching, the nymphs begin to feed on the seeds of the plant. They thrust their beaks into the dry seeds and apparently obtain their nourishment by injecting saliva into the seeds, which dissolves the solid material there so that they can suck it up into the body. The entire nymphal stage is spent in feeding on the dry seeds, a very remarkable and interesting adaptation. Due to the work of *L. phragmitella* and *D. julianalis*, the seeds of many of the old heads are kept from being scattered by the winter storms, and *Ischnorrhynchus resedae* simply takes advantage of these

conditions. It inserts its eggs into the pappus, where they are hidden from all enemies and where the nymphs find an abundance of food at hand which is not contested by any close relatives and which, indeed, is used by few other insects.

INSECT INHABITANTS OF THE LEAF OF TYPHA

The inhabitants of the leaf comprise two classes, the surface feeders and the leaf miners. The surface feeders include, among the Lepidoptera, *Arsilonche albovenosa*, and among the Hemiptera, the Aphidae enumerated on page 501. The most common of the surface feeders is the noctuid caterpillar, *A. albovenosa*. It is a general feeder but is very commonly found on cat-tail. The eggs are placed on the upper part of the leaf, and the larvae, as soon as hatched, feed on the leaf. A leaf thus infested has the appearance of having been skeletonized. After they grow larger, the larvae begin feeding on the edge of the leaf, where they eat out large sections.

The species of aphids mentioned on pages 500–501 may be classed as feeders on the leaf, although they occasionally feed lower down on the stem and sheaths of the plant.

The leaf miners include *Arzama obliqua* Walk. and *Nonagria oblonga* Grote. These two noctuid larvae do not restrict themselves entirely to leaf mining but they begin their larval life as leaf miners, later becoming true stem borers. Although the two species are related, their habits differ greatly. *A. obliqua* overwinters as a larva in its burrow in the cat-tail plant, whereas *N. oblonga* apparently passes the winter in the egg stage. The eggs of *A. obliqua* are laid in the spring, while those of *N. oblonga* are apparently laid in the fall. The young larvae of *A. obliqua* burrow gregariously, but the larvae of *N. oblonga* are solitary miners. The nature of their mines, too, is very different. *A. obliqua* advances down the channels of the leaf, leaving the longitudinal partitions of the leaf intact and only destroying the cross partitions, while *N. oblonga* produces a sort of blotch mine by zigzagging back and forth in the leaf and destroying both the longitudinal and the transverse partitions. Both species feed mainly on the chlorophyll of the leaf. When ready for the first molt, *A. obliqua* sheds its skin at once, right in the mine, near the healthy, undisturbed, succulent tissue of the leaf; but *N. oblonga*, when ready for its first molt, first severs the connecting tissue of the leaf in order to

produce a drier situation in which to cast off its coat. This variation indicates that *A. obliqua* is better adapted than *N. oblonga* to live in moist or wet situations. A comparison of the tracheal systems of the two larvae shows this yet more clearly. *A. obliqua* has the spiracles of the eighth abdominal segment located on the dorsal surface and they are more than twice the size of the other spiracles of the body. Directly attached to these spiracles are the two longitudinal tracheal trunks of the body. Segment 9 of the abdomen is flattened dorsally so as to be only half as thick dorso-ventrally as the other abdominal segments, thus making room for the large spiracles on the eighth segment. This allows the body of the larva to be almost entirely submerged in the water, for as long as these spiracles remain above the surface it suffers no harm. The tracheal system of *N. oblonga* has not undergone any such modifications, however. The spiracles on its eighth abdominal segment are located in the natural position and are the same size as the other abdominal spiracles. Consequently the larva is likely to suffer harm if much water gathers in the burrow, as often occurs in wet situations. The larvae of *A. obliqua* remain in the leaf of Typha only through the first instar, while the larvae of *N. oblonga* often remain in the leaf through the second and even the third instar. The nature of their mining habits may have much to do with the difference. *A. obliqua* does not destroy the longitudinal partitions of the cat-tail leaf, and consequently must get out after its first molt on account of its increased size in the second stage. *N. oblonga*, however, cuts through the partitions in any direction and so is able to remain in the leaf for a longer period. After leaving the leaf, both larvae become solitary borers in the stalks of cat-tail.

INSECT INHABITANTS OF THE STALK OF TYPHA

The insects which work in the stalks of the cat-tail include two species of the Lepidoptera, *Arzama obliqua* Walk. and *Nonagria oblonga* Grote, and the Coleoptera, *Calendra pertinax* Oliv. and *Notaris puncticollis* Lec.

After the larvae of *A. obliqua* and *N. oblonga* leave the mines of the leaf, they become stem borers. Their methods of entering the stem are very similar. Both are frequently found feeding for a time behind the sheaths of the outer leaves of the plant. From the sheath they either bore directly into the stem or enter from between the leaves of the leaf bundle. Both work their way to the center of the plant and locate at

the point where the tender new tissue is forming. The effect of their work on the plant is very similar: the central leaves of the leaf bundle die and the plant fails to produce a fruiting stalk.

C. pertinax, the weevil, begins its larval life as a stem borer, later becoming a borer in the rhizome of the plant. The eggs of *C. pertinax* are inserted into the sheaths of the plant, near the ground. The newly hatched larvae bore to the center of the stalk and hollow it out just above the crown, thus arresting the further growth of the plant. After feeding on the tender tissue at the center of the stem for some time, the larvae enter the rhizome and there feed on the more substantial starchy food. When full-grown, the larvae return to the stalk and there form a pupal chamber in which the transformation takes place. There is only one generation. The larvae are ordinarily solitary borers, although as many as seven larvae have been found in one plant.

INSECT INHABITANTS OF THE RHIZOME OF TYPHA

The inhabitants of the rhizome are the Coleoptera, *Calendra pertinax* Oliv. and probably *Notaris puncticollis* Lec. The larvae of *C. pertinax* feed during the major part of their larval period on the starchy core in the rhizome of the plant. By first tunneling out the center of the stalk at the crown of the plant, they prevent the formation of new leaves, and in this way the larvae cause the starch to remain in the rhizome for their nutriment which would otherwise be used up in the growth of the plant. The leaves already formed are left undistrubed to manufacture and send down more starch to the rhizome. Very likely the habits of *N. puncticollis* are similar to those of *C. pertinax*.

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PLATE XXXIX

TYPHA LATIFOLIA

1, Sterile seed, showing large size of pericarp. 2, Fertile seed. (The pericarp fits closely over the kernel.) 3, Seed, or kernel, removed from pericarp. 4, Embryo protruding through pericarp. 5, Same as 4, with pericarp removed. 6, Growing embryo as it appears when removed from seed. 7, Embryo pushing open cap of seed. 8, Beginning of formation of root. (The arrow indicates the developing leaf.) 9, Further development of young plant. (The leaf has protruded and root hairs have developed on the root.) 10, Young plant with three leaves and three roots, showing disintegration of tip of first leaf, whereby it frees itself from the seed

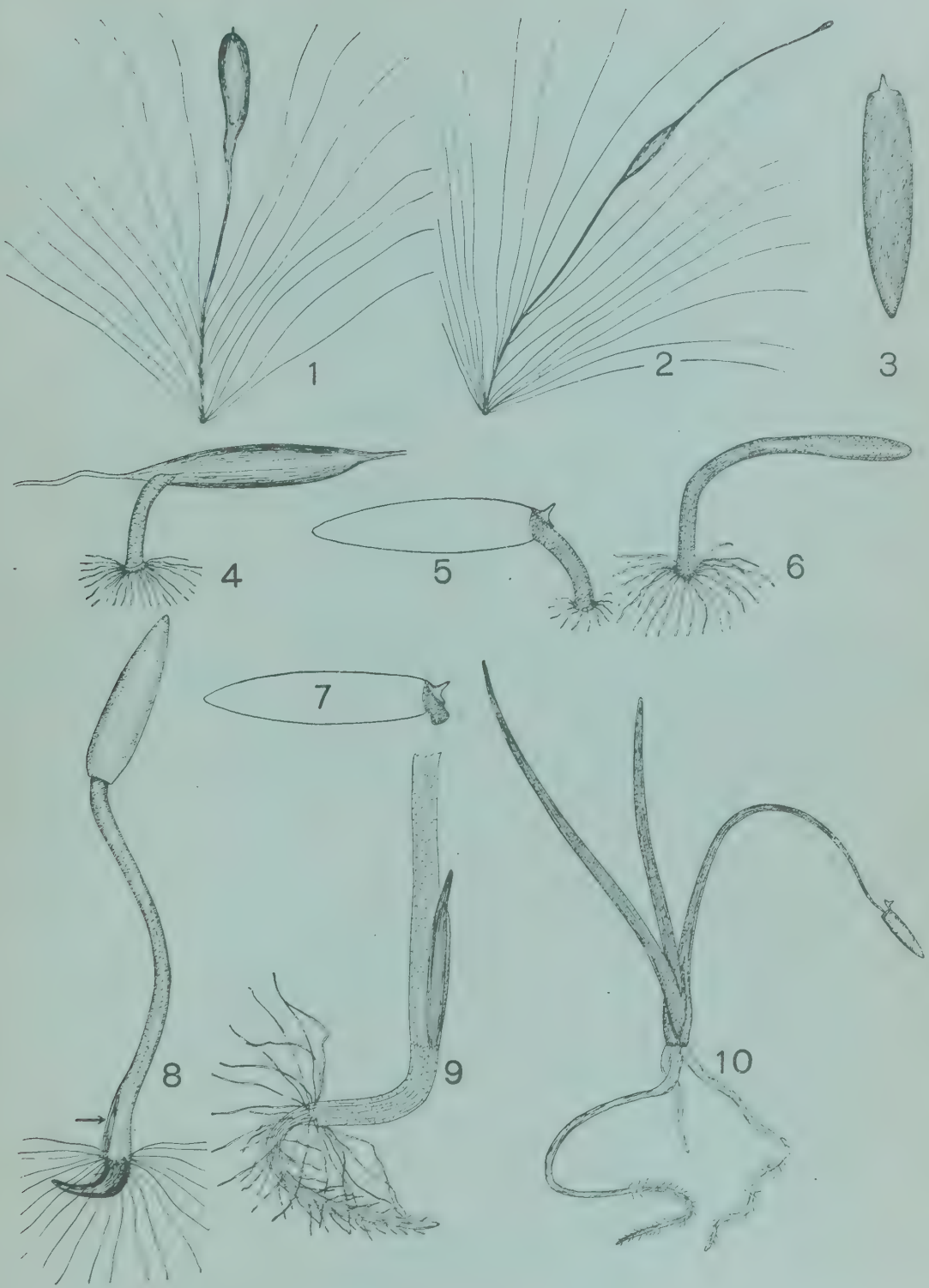
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PLATE XL

TYPHA LATIFOLIA AND CALENDRA PERTINAX

Typha latifolia: 11, Cross section of leaf. 12, Cross section of a small part of leaf, showing more detail. 13, Cells of rhizome filled with starch grains. (Dormant season.) 14, Part of 12 enlarged to show structure of epidermis, chlorophyll, supporting tissue, and vascular bundles. 15, Cells of rhizome partly filled with starch grains. (Growing season.) 18, New offsets

Calendra pertinax: 16, Egg. 17, Egg inserted in sheath of cat-tail. 19, Rhizome of cat-tail cut open to show larval work. 20, Newly hatched larva

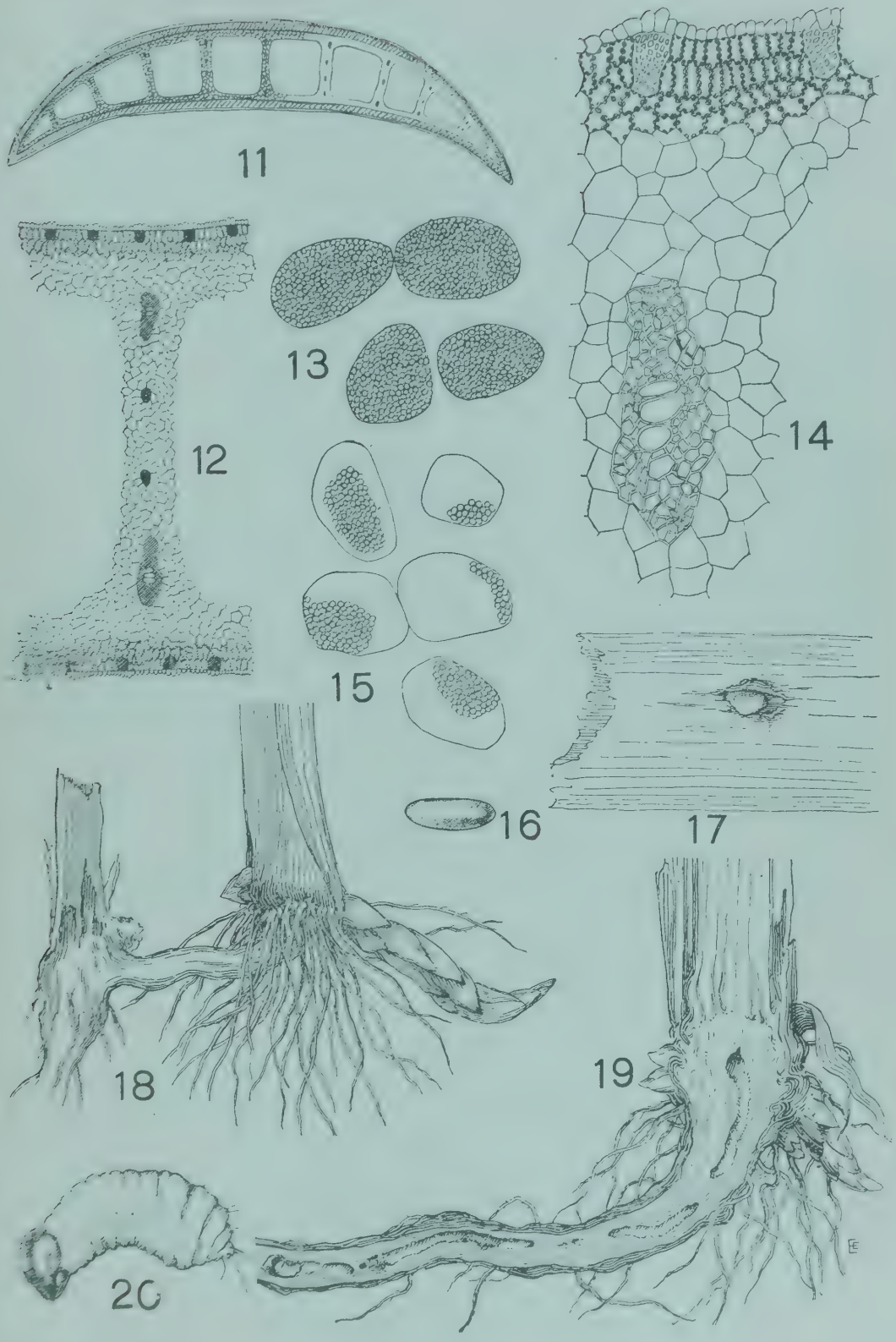
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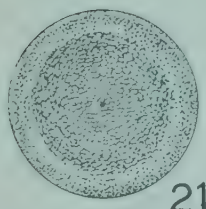
PLATE XLI

ARZAMA OBLIQUA

21, Egg. 22, Full-grown larva. 23, Pupa. 24, Egg mass on cat-tail leaf. (The larvae have emerged and mined along the middle part of the leaf, thus causing the center to die.) 25, Cat-tail leaf with egg mass, showing mine and exit holes of larvae. 26, Adult female. 27 and 28, Full-grown overwintering larvae in stalks of cat-tail. 29, Newly hatched larva. 30, Dorsal view of caudal segments of larva, showing position of spiracles on eighth abdominal segment. 31, Tracheal system of full-grown larva. (Only the first one of the five branched tracheal tubes is shown in its entire length)



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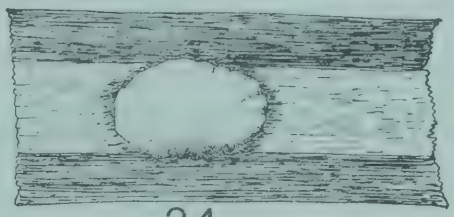

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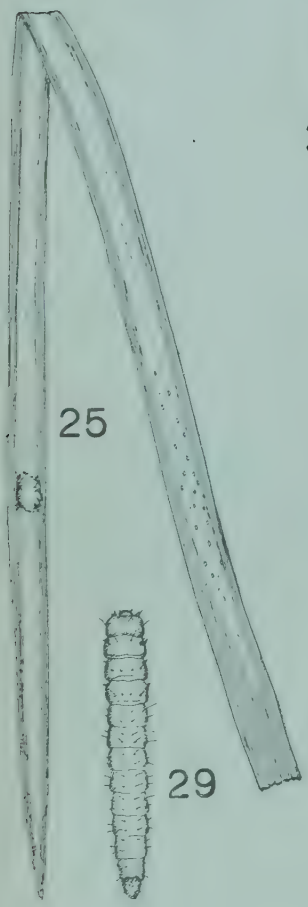

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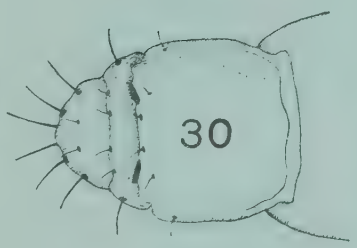

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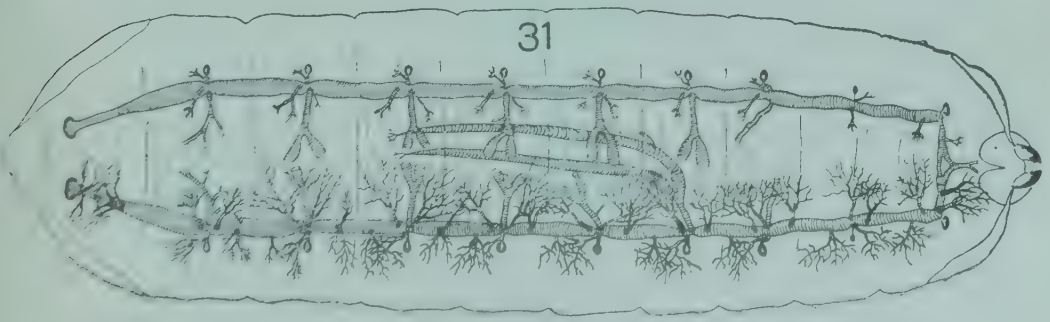

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PLATE XLII

LYMNAECIA PHRAGMITELLA AND NONAGRIA OBLONGA

Lymnaecia phragmitella: 32, Full-grown larva. 34, Pupa. 35, Stalk of cat-tail with leaf turned aside to show where larvae have tunneled in, preparatory to pupation

Nonagria oblonga: 33, Pupa. 36, Cat-tail plant showing work of larvae. (The first-stage larvae have cut the leaf. A mine appears also in the outer sheath.) 37, Cat-tail leaf showing early larval work. (The arrow points to the cast skin of the first molt in the transverse mine)

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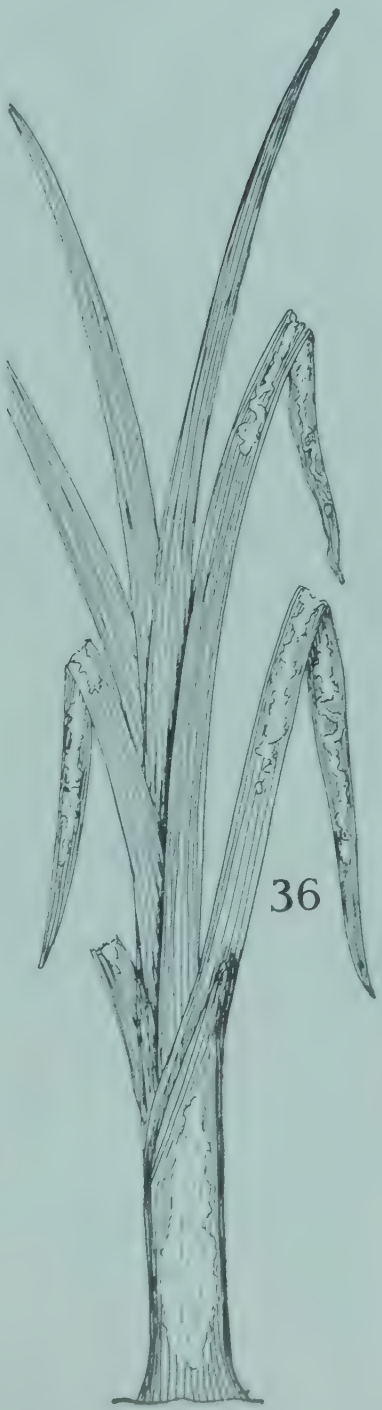

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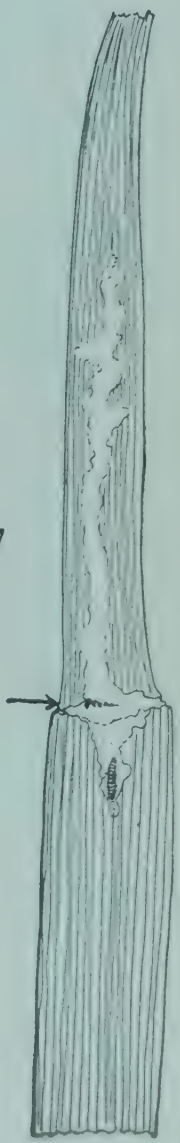

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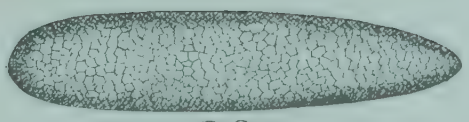
PLATE XLIII

DICYMOLOMIA JULIANALIS

38, Egg. 39, Reticulations on surface of egg. 40, Newly hatched larva. 41, Full-grown larva. 42, Axis of cat-tail head cut open to show larval work. 43, Axis of cat-tail head, showing opening of larval tunnels. 44, Pupa. 45, Cross section of head of cat-tail, showing location of eggs (indicated by *a*). 46, Empty egg shell after emergence of larva



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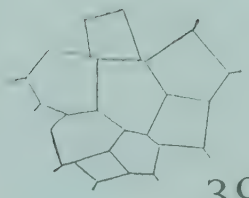

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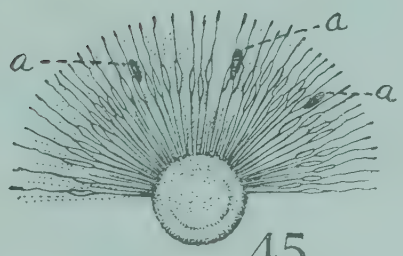

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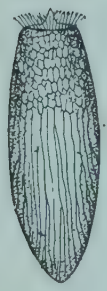
PLATE XLIV

ISCHNORRHYNCHUS RESEDAE

47, Egg. 48, First-stage nymph. 49, Fourth-stage nymph. 50, Third-stage nymph. 51, Second-stage nymph. 52, Adult female. 53, Enlarged drawing of beak of nymph inserted in seed of cat-tail. 54, First-stage nymph. 55, Fifth-stage nymph feeding on seed of cat-tail



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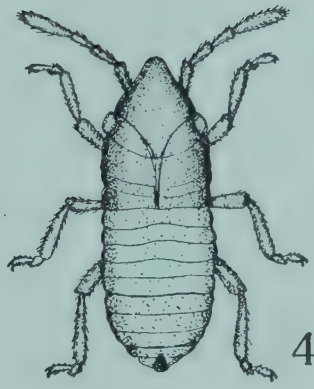

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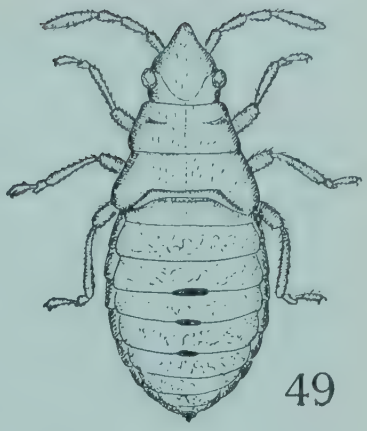

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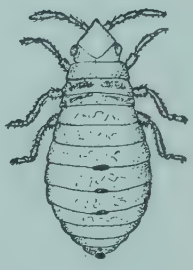

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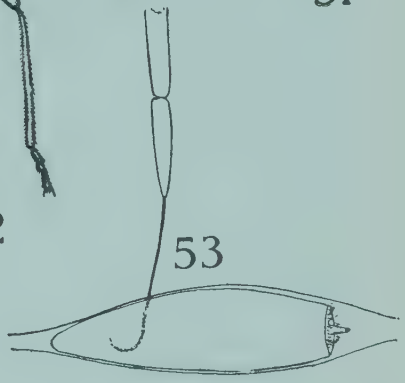

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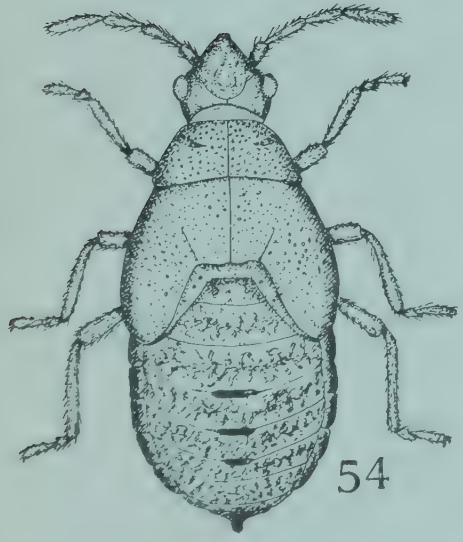

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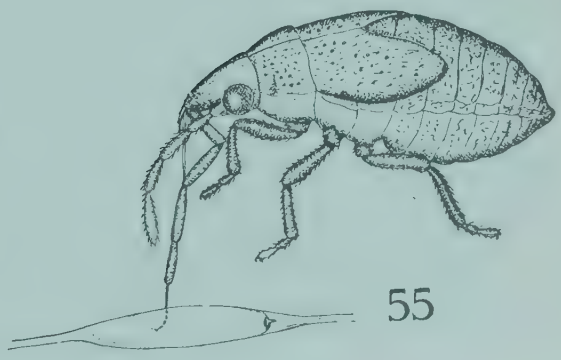

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PLATE XLV

TYPHA LATIFOLIA

56, Two plants connected by underground rhizome, showing also new offsets at bases of old plants. 57, Two pieces of rhizome with outer covering removed to show the relative size of the central starchy core. 58, Leaf with part of the upper epidermis removed to show the structure. 59, Cat-tail heads as they appear in late fall. (The one on the left is infested with the larvae of *Lymnaecia phragmitella;* the one on the right is uninfested.) 60, Cross section of a rhizome

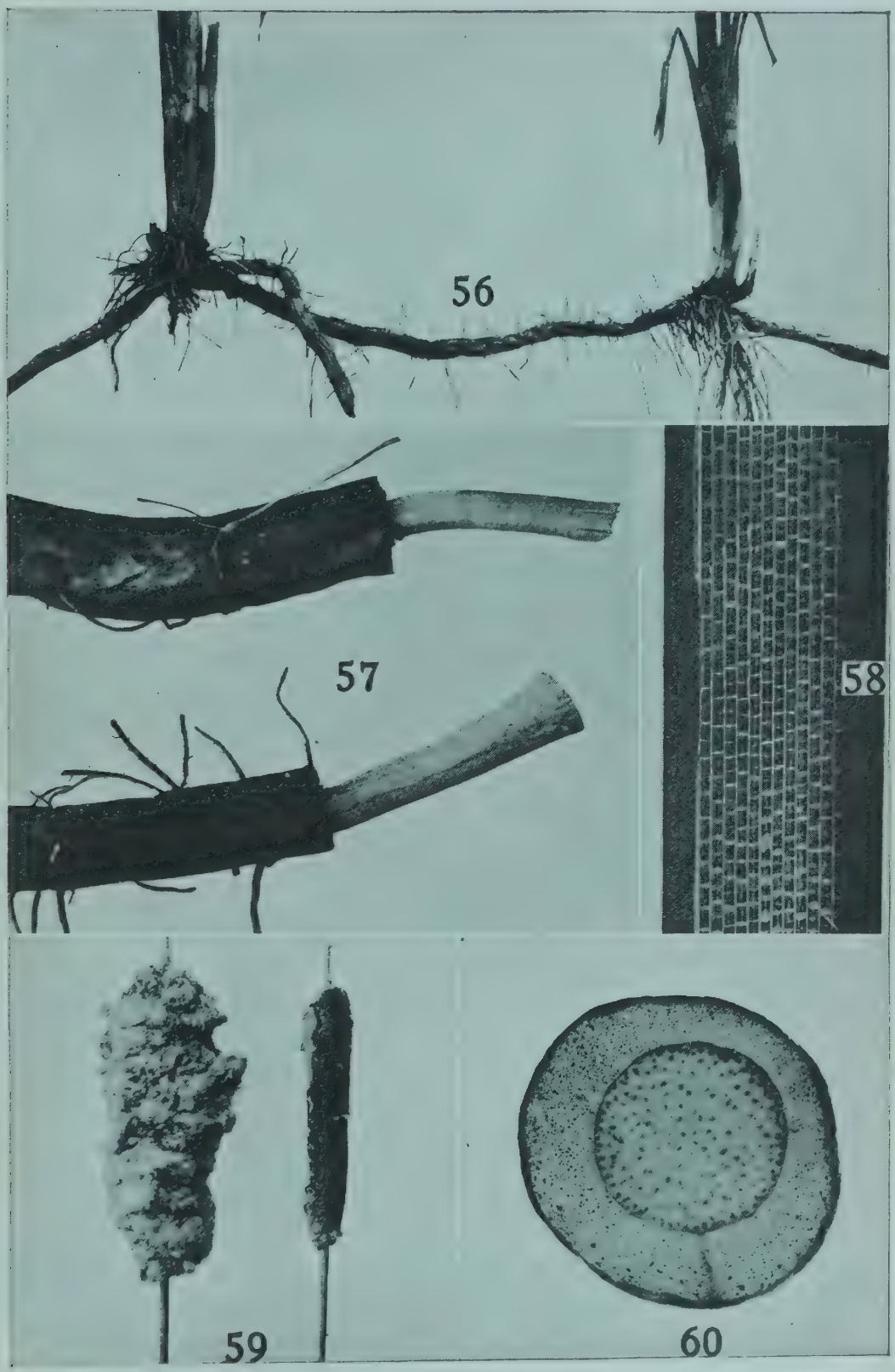
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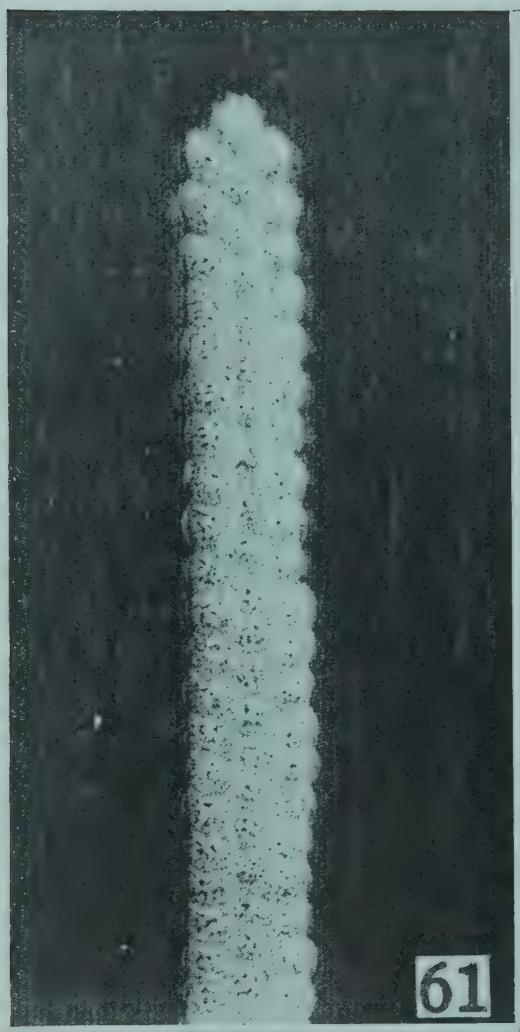
PLATE XLVI

ARSILONCHE ALBOVENOSA AND ARZAMA OBLIQUA

Arsilonche albovenosa: 61, Eggs. 62, Larva feeding on cat-tail leaf. 63, Pupa. 64, Adult
Arzama obliqua: 65, Egg mass. 66, Full-grown larva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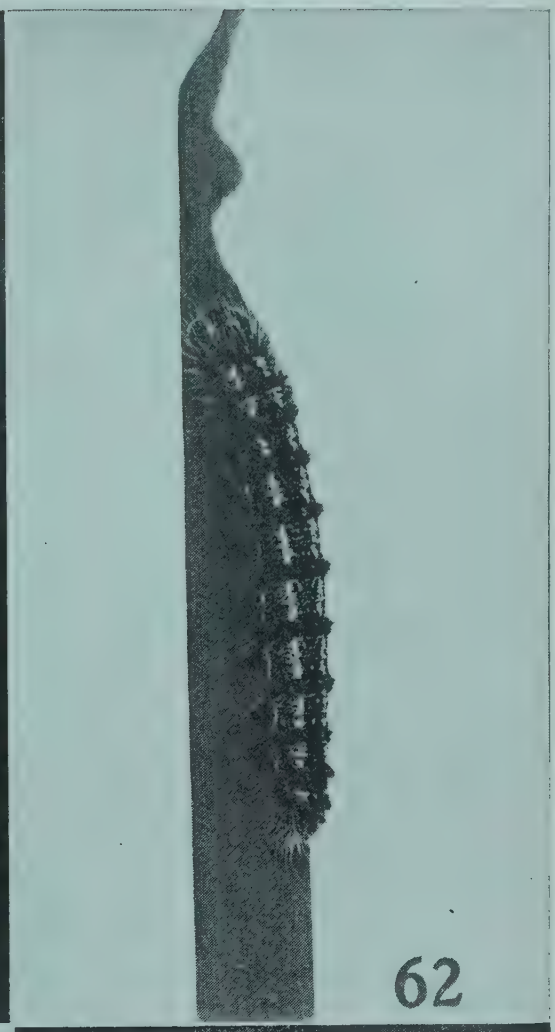
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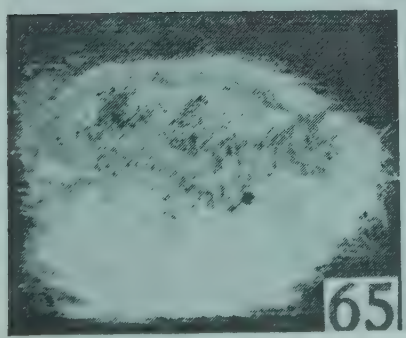
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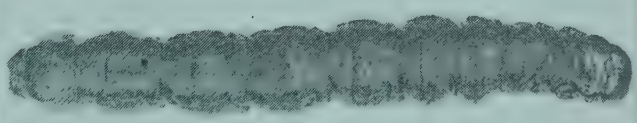
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PLATE XLVII

NONAGRIA OBLONGA AND ARCHIPS OBSOLETANA

Nonagria oblonga: 67, Full-grown larva. 68, Adult. 70, Larva in tunnel in stalk of cat-tail. 71, Pupa

Archips obsoletana: 69, Young cat-tail head showing larval work. (The covering is pulled aside, revealing the head of the larva underneath.) 72, Young cat-tail head showing larval work. (The stigmas of the pistillate flowers are tied together to form a covering for the larva.) 73, Appearance of cat-tail head after wind has torn off covering made by larvae. 74, Pupa. 75, Adult. 76, Larva

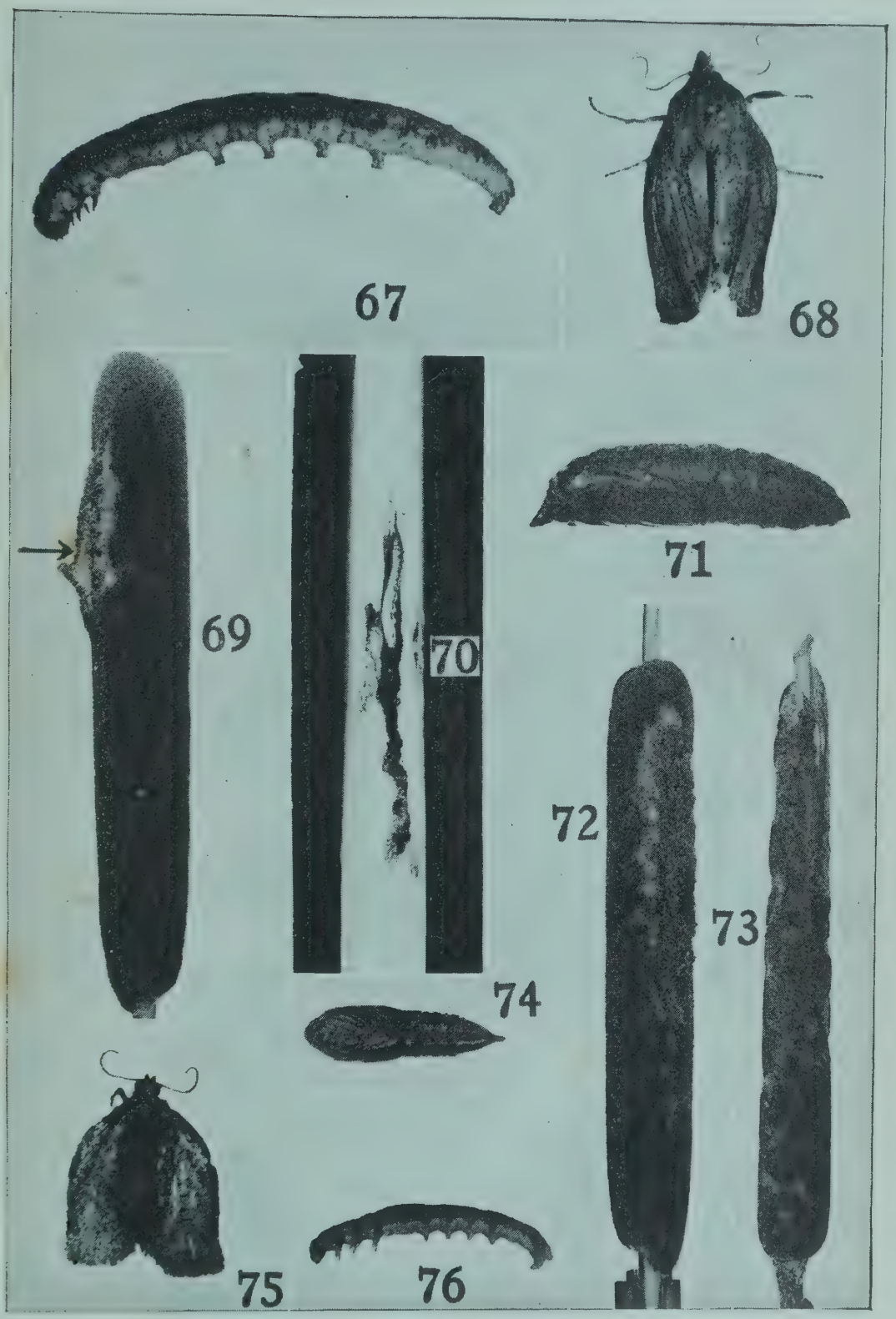
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PLATE XLVIII

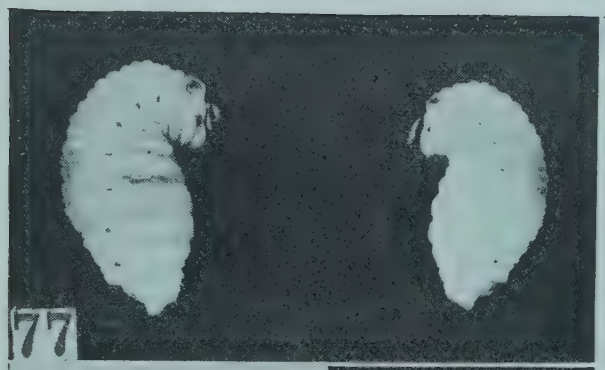
CALENDRA PERTINAX, DICYMOLOMIA JULIANALIS, LYMNAECIA PHRAGMITELLA, AND NOTARIS PUNCTICOLLIS

Calendra pertinax: 77, Larvae. 78, Adult. 79, Pupa. 80, Pupa in burrow in stalk of cat-tail

Dicymolomia julianalis: 81, Adult

Lymnaecia phragmitella: 82, Cocoons removed from cat-tail head. (One is cut open to show pupa inside)

Notaris puncticollis: 83, Adult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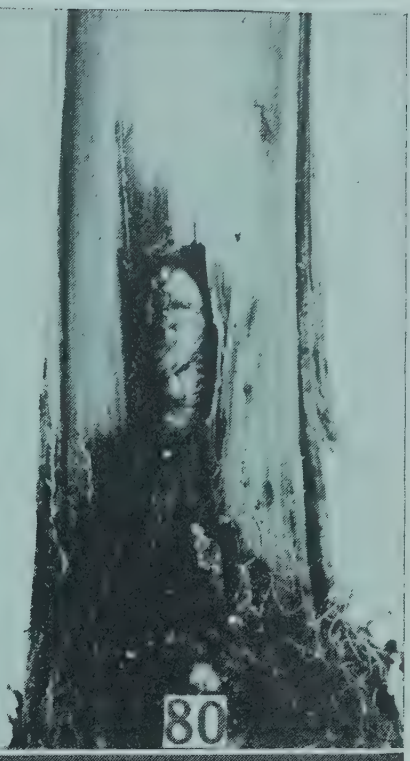
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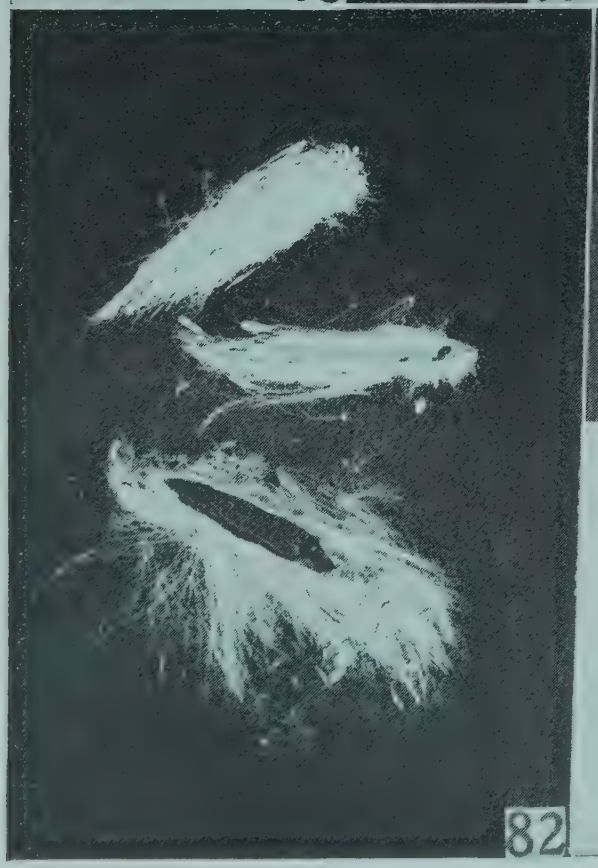
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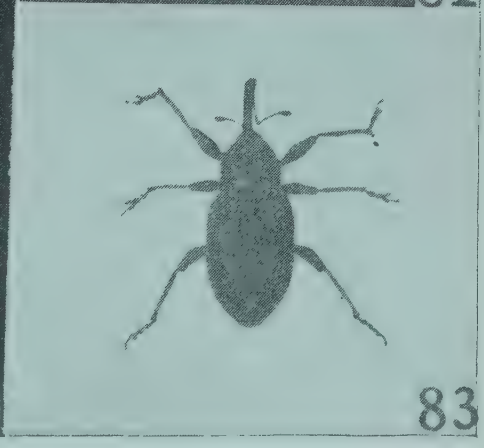
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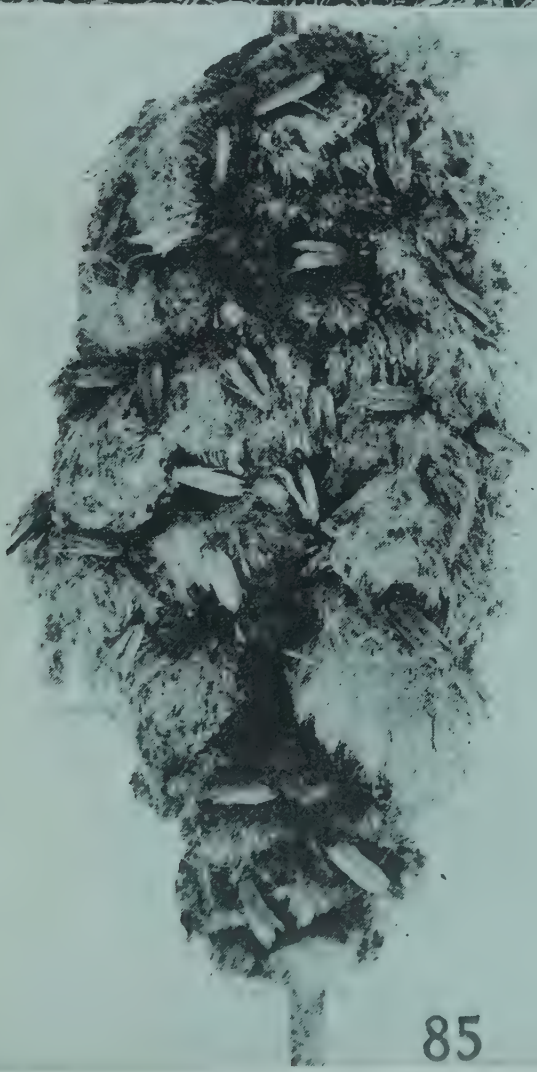
PLATE XLIX

TYPHA LATIFOLIA

84, A cat-tail patch in July, showing the large number of fluffy heads which are infested with the larvae of *Lymnaecia phragmitella*. 85, Laboratory cat-tail head on which adults of *L. phragmitella* are resting. 86, Nearly mature head of cat-tail, showing evidence of work of young larvae of *L. phragmitella* and *Dicymolomia julianalis*



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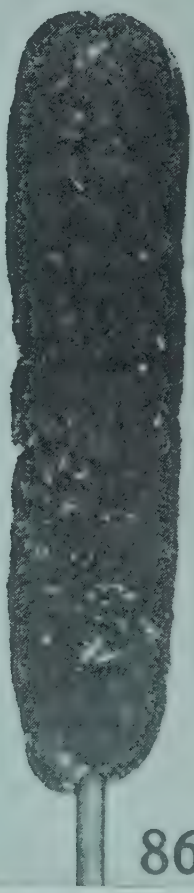

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CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

THE INHERITANCE OF SALMON SILK COLOR IN MAIZE

E. G. ANDERSON

ITHACA, NEW YORK
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CONTENTS

PAGE

Nomenclature 539
Description of silk colors 540
Preliminary studies and indications 541
Analysis of inheritance 542
Interrelations of green, salmon, and brown silks 542
Relation of salmon silks to pericarp color 542
Relation of salmon silks to the *B* and *Pl* factors for plant color 545
Relation of salmon silks to the *A* factor 546
Relation of salmon silks to the *R* factor 546
Summary of inheritance 547
Linkage relations of *Y*, *Pl*, and *Sm* 547
Preliminary tests of linkage of *Pl* and *Sm* 547
Construction and results of three-point tests 548
The chromosome map 549
Coincidence of crossing-over 553
Summary of linkage studies 554
Literature cited 554

THE INHERITANCE OF SALMON SILK COLOR IN MAIZE

THE INHERITANCE OF SALMON SILK COLOR IN MAIZE[1]

E. G. Anderson

At the Nebraska State Corn Show of 1908, a number of odd types of corn were gathered together to form a "freak" class. Among them was a "Bronze Pop Corn," so named became of a light bronze color in the pericarp. This ear was obtained by Professor R. A. Emerson, after the exhibit was over, in order to study the inheritance of that pericarp color. The plants grown therefrom were also characterized by brown or brownish silks (Plate LIII). An outcross gave green silks in the F_1. From brown-silked segregates in the progeny of this cross, a true-breeding stock was again obtained. This stock was used in crosses for a study of the inheritance of pericarp color. In one small F_2 of only five plants, there appeared three with green silks and one with brown. The fifth plant had very brilliant salmon or orange-colored silks (Plate LII). This plant was a dilute sun red with red pericarp. It was crossed with red, green, and brown silk colors, and with a purple plant having brown silks. F_1's were grown and selfed to obtain F_2 progenies. The crosses with red and with green silks gave in F_1 red and green silks, respectively. The cross with brown silks gave salmon.

In order to devote more time to studies on aleurone and plant colors and other problems, Dr. Emerson at this point requested the writer to take up the study of these silk colors and their relation to other characters in maize. In his further studies the writer has had the advantage of the hearty cooperation and ever-ready suggestions of Dr. Emerson, and he wishes to acknowledge his sincere gratitude for this help and encouragement.

NOMENCLATURE

The factors referred to in this paper, together with the factor symbols used, are given in the following list:

A a — Anthocyanin pigment. A factor pair for pigmentation of aleurone, sheaths, leaves, anthers, and so forth. (Emerson, 1918, 1921.)

B b — Brown plant color. A factor pair for leaf and sheath pigmentation. (Emerson, 1921.)

[1] Paper No. 83, Department of Plant Breeding, Cornell University, Ithaca, New York.

Pl pl — Purple anthers. A factor pair for pigmentation of anthers sheaths, pericarp, and so forth. (Emerson, 1921.)

These three factor pairs interact to give the following plant color types described by Emerson (1921):

A B Pl — Purple
A B pl — Sun red
A b Pl — Dilute purple
A b pl — Dilute sun red
a B Pl — Brown
a B pl — Green
a b Pl — Green
a b pl — Green

R^r R^g r^r r^g r^{ch} — Red aleurone. A series of allelomorphs affecting anthocyanin pigmentation in aleurone, sheaths, leaves, pericarp, anthers, and silks. (East and Hayes, 1911; Emerson, 1918, 1921.)

P p — Pericarp color. Two of a series of allelomorphs for pericarp coloration. (Emerson, 1911.) The bronze type was so pale in color that it could not be satisfactorily distinguished from white (colorless). Only two symbols are used herein, *P* for red pericarp and *p* for white or bronze pericarp.

Y y — Yellow endosperm. (East and Hayes, 1911; Emerson, 1921.)

Sm sm — Salmon silk color. Described in this paper.

DESCRIPTION OF SILK COLORS

The colors of silk in maize may be described as follows:

1. Green (Plate L). Silks light green, paler below husks; varying from a pure pale green to yellowish green.

2. Red (Plate LI). Silks green, as above, with the addition of a red anthocyanin pigment where exposed to light. The amount of red pigment may vary from a slight trace in the hairs, to sufficient to obscure the green color, giving the silks a deep or dark red color. The darker red silks frequently have some red below the husks. Emerson (1921) has shown this color to be due to the *R* factor. Microscopic sections show anthocyanin pigment in peripheral parts of the silks.[2]

[2] The microscopic sections are prepared as follows: Pigmented tissue is fixed for from twelve to twenty-four hours in a saturated solution of mercuric chloride in 95-per-cent alcohol, and washed with 95-per-cent alcohol without iodine. The usual paraffin method of embedding and sectioning is followed and the preparations are mounted in balsam without staining. Sections from 15 to 25 microns in thickness have proved satisfactory.

BROWN SILKS

The color develops in both exposed and protected parts of the silks
(Drawing by Carrie M. Preston)

SALMON SILKS

The color develops beneath the husks as well as in exposed parts of the silks
(Drawing by Bernice M. Branson)

RED SILKS

The red pigment develops only in the parts of the silks exposed to the light
(Drawing by Carrie M. Preston)

GREEN SILKS

Silks of this type may be associated with any plant-color type. Purple husks are shown here for contrast

(Drawing by Carrie M. Preston)

3. Salmon (Plate LII). Silks light salmon-orange to salmon. The color below the husks is similar to that of exposed parts. Microscopic sections show only a faint brownish cast to the tissues thruout the silks.

4. Brown (Plate LIII). Silks orange-pink to pale salmon or salmon-buff in both exposed and covered parts. Salmon and brown silks intergrade, forming a continuous series. The lighter forms are difficult to distinguish from the yellowish green silks of No. 1. Both salmon and brown silks may have red anthocyanin pigment present, as in No. 2.

PRELIMINARY STUDIES AND INDICATIONS

Previous tests had shown salmon silk color to be recessive to green and at least partially dominant to brown. Crosses of salmon and brown did not give green color in the F_1. This was taken to indicate that these colors were recessive for a common factor. The anthocyanin pigment present in red silks was shown to be inherited separately by the occurrence of all combination classes (green-red, green, salmon-red, and salmon) in the F_2 of red x salmon.

From observation of cultures previously grown, both salmon and brown silks were known to occur on dilute sun red, on sun red, and on purple plants. Their occurrence on brown or green plants had not been recorded. Microscopic examination of the pigments of maize had shown the presence of a purple-red anthocyanin pigment in purple, sun red, dilute purple, and dilute sun red plants. When the *A* factor is recessive, no anthocyanin develops (except traces in the shank and the inner husks of brown plants). Instead, a yellow or brownish pigment may be formed. A similar relation holds with the pericarp pigments. Red pericarp color is due to an orange-red or brick-red pigment. Its homolog with recessive *A* is yellowish brown, similar in appearance to the brown plant-color pigment. The quantity of pigment in salmon silks is so small that microscopic sections gave little information. But the color of the salmon silks was so similar to the color of thin sections of red pericarp as to suggest the possible identity of the pigments. The brown silk might, it was thought, be only a dilute form of salmon. These suggestions were further strengthened by the fact that the original salmon-silked plant had red pericarp and that the brown silks had been obtained from a plant with bronze

pericarp. Sections of this bronze pericarp showed a small amount of orange pigment.

With these suggestions in mind as a working basis, experiments were planned to test them.

ANALYSIS OF INHERITANCE

Interrelations of green, salmon, and brown silks

The indications just mentioned, regarding the relationships of these silk colors, were all checked and corroborated by further tests. Crosses of green with salmon gave green in the first generation, segregating green and salmon, or green, salmon, and brown, in the second. The distinction between salmon and brown was not sharp. With the small numbers used in these tests, the numbers approach a simple ratio of 3 greens to 1 salmon or to 1 salmon and brown.

Crosses between green and brown likewise gave green, segregating in the F_2 into green and brown or in some cases into green, salmon, and brown. In either case there was about 75 per cent of greens.

Crosses of salmon with brown gave salmon. The F_2 ranged from salmon to brown, with salmon predominating.

These results show that there is a common factor pair which differentiates between green on the one hand and salmon and brown on the other. This pair is herein referred to as the salmon-silk factor pair and is designated by the symbols *Sm sm*.

The difference between salmon and brown silks is not explained by these simple tests, tho the occurrence of brown silks in the progenies of outcrosses of salmon, and vice versa, is at least a strong indication of one or more modifying factors.

Relation of salmon silks to pericarp color

In order to test the relationship of the salmon factor to the factor for pericarp color, two series of crosses were made. In the first, a colored-pericarp, green-silked plant (*P Sm*) was crossed with a light-bronze-pericarp, brown-silked plant (*p sm*). In the second, two white-pericarp green-silked plants (*p Sm*) were crossed with the original salmon-silked plant, which had red pericarp (*P sm*). The F_1's were crossed with the double recessive. The results are given in table 1:

TABLE 1. RELATION OF SALMON SILKS TO PERICARP COLOR

I. Backcrosses of *P Sm* x *p sm* with *p sm*

Pedigree no.	*P Sm*	*P sm*	*p Sm*	*p sm*	Total
253–4	9	6	11	20	
255	5	11	12	10	
256	9	6	15	7	
777–8	41	32	41	39	
Totals	64	55	79	76	274

Observed per cent of recombinations.....48.9
Per cent expected with independent segregation.....50.0±2.0

II. Backcrosses of *p Sm* x *P sm* with *p sm*

Pedigree no.	*P Sm*	*P sm*	*p Sm*	*p sm*	Total
238–9	43	61	51	53	
241–2	31	28	31	38	
779–80	23	25	25	28	
781–2	43	40	50	40	
Totals	140	154	157	159	610

Observed per cent of recombinations.....48.9
Per cent expected with independent segregation.....50.0±1.4

The observed per cent of recombinations is 48.9 in both series, which is in very close agreement with the expectancy for independent segregation of *P* and *Sm*.

In order to determine the possible relation of pericarp color to the difference between salmon and brown silks, a light-pericarp, brown-silked plant was crossed with a red-pericarp salmon. This was backcrossed

with a light-pericarp, brown-silked plant similar to the one parent. The silk colors were noted during the summer. It was impossible to make any sharp separations, for the colors varied from a deep salmon to a typical or even light brown. The presence of red anthocyanin pigment added to the difficulty, as did also the fact that the silks could not be noted at the same stage. So they were only roughly classified, the classifications from time to time not being entirely comparable. The notes were underscored for a number of good salmons and browns. The pericarp colors were determined in the fall. The results are given in table 2:

TABLE 2. BACKCROSSES OF *p, sm* x *P sm* WITH *p sm*

Silk color	Red pericarp	White or light bronze
Salmon, underscored	17	0
Salmon	167	19
Salmon—	25	10
Salmon-brown	33	11
Brown-salmon	10	24
Brown+	24	65
Brown	11	172
Brown, underscored	0	44

It will be seen from this table that most of the red-pericarp plants had been noted as having salmon silks, while the light-pericarp ones were mostly noted as having brown silks. It is also significant that, of those cases in which salmon was underscored, all had red pericarp. Likewise, of the cases in which brown was underscored, all had light pericarp. Since the salmon factor pair *Sm sm* has been shown to segregate independently of the factor pair *P p* for pericarp color, this variation cannot be due to the *Sm sm* pair. The conclusion is drawn that the intensity of pigmentation of silks recessive for *sm* is largely a function of the intensity of pigmentation of the pericarp or of some factor closely associated with the factor for pericarp color. The former view is substantiated

by the fact that no selfed progenies from light-pericarp plants have ever given any good salmon silks, while progenies from red-pericarp plants have always given some salmon silks even tho the parents had been noted otherwise. No brown silks have been found in families breeding true for red pericarp.

Relation of salmon silks to the B and Pl factors for plant color

Several crosses made with salmon silks involved the *B* factor. Both F_1 combinations, *B Sm* x *b sm* and *B sm* x *b Sm*, were backcrossed with the double recessive. The results (table 3) show independent segregation of these factors.

TABLE 3, RELATION OF SALMON SILKS TO THE *B* AND *Pl* FACTORS FOR PLANT COLOR

I. Backcrosses of *B Sm* x *b sm* with *b sm*

Pedigree no.	*B Sm*	*B sm*	*b Sm*	*b sm*	Total
241–2	25	24	39	41	
779–80	21	19	28	35	
Totals	46	43	67	76	232

Observed per cent of recombinations 47.4
Per cent expected with independent segregation ..... 50.0±2.2

II. Backcrosses of *B sm* x *b Sm* with *b sm*

Pedigree no.	*B Sm*	*B sm*	*b Sm*	*b sm*	Total
774–6	78	62	80	53	273

Observed per cent of recombinations 47.6
Per cent expected with independent segregation ..... 50.0±2.0

One of the crosses of the original salmon-silked plant, *A b pl sm*, was with a purple plant with green silks, *A B Pl Sm*, related to the bronze stock. The progeny consisted of purple and sun red plants with green and salmon silks, showing the parent to have been heterozygous for both *Pl* and *Sm*. Two small plantings gave the following distributions: *Pl Sm*, 26; *Pl sm*, 7; *pl Sm*, 4; *pl sm*, 23; whereas equality of the four classes would be expected if the factors were independent. This was obviously a linkage relation. The factor *Pl* was known to be linked with a factor *Y* for yellow endosperm (Emerson, 1921). Tests of the linkage relations within this group are given in a later section of this paper.

Relation of salmon silks to the A factor

From an outcross of the original salmon-silked plant with one heterozygous for brown silks and for the *A* factor, several plants were selfed. One sun red plant was homozygous recessive for the salmon silk factor and heterozygous for *A* and *B*. Thirty-four sun red and dilute sun red plants had salmon or brown silks. Two others were first noted as green but were presumably a light brown, both having white pericarp. Eleven green plants appeared, all having green silks. Later observations on green and brown plants of other families segregating for both *a* and *sm* have likewise failed to reveal any green plants with other than green silks. That this is not due to linkage is shown by the linkage of *Sm* with the *Pl* factor, which is known to be independent of *A*, and by the fact that the green plants have green silks in families that are homozygous recessive *sm*.

Relation of salmon silks to the R factor

Two questions of interest arose regarding the relation of salmon silk color to the *R* series of allelomorphs. The first was the relation of cherry pericarp color to the intensity of color in salmon or brown silks; the second was the possibility of the occurrence of salmon silks on green plants of the constitution R^g *A b Pl* or R^g *A b pl*.

To test the effect of cherry pericarp, a sun red with brown silks, *A B pl sm* r^r, was crossed with a dilute purple with cherry pericarp and green silks, *A b Pl Sm* r^{ch}. Backcrosses gave a few plants with cherry pericarp and brown silks. They were not noticeably different in silk color from the white-pericarp plants of the same families.

To test for the occurrence of salmon silks on green plants of the constitution *R^g A b Pl* or *R^g A b pl*, a dilute purple plant with salmon silks was crossed with a green plant of the constitution *R^g A b pl*. Two of the F_1 plants were selfed. Purple seeds only were planted. These gave 44 dilute purples and dilute sun reds, of which 32 had green silks and 12 had salmon. There were 25 green plants, *R^g A b*, 18 of which had green silks; the other 7 had typical salmon and brown silks.

From these two tests, it may be concluded that salmon silk color is not dependent on the *R* factor nor is it noticeably influenced thereby. This is similar to the relation between red pericarp color and *R^g* (Emerson, 1921).

Summary of inheritance

Salmon and brown silks are recessive to green silks by a single factor pair, *Sm sm*.

This factor, *Sm*, is independent in inheritance from *P* (pericarp), *A* (aleurone and plant color), *B* (plant color), and *R* (aleurone, plant color, cherry pericarp, and red silk color).

It is linked with the factor *Pl* (plant color), and consequently also with *Y* (yellow endosperm).

Dominant *A* is necessary for the production of salmon or brown silk color; that is, the combination *a a sm sm* is green.

The intensity of pigmentation of salmon-brown silks is directly related to the intensity of pigmentation of the pericarp.

The relation of the factors *A*, *Sm*, and *P* to silk color may be represented schematically as follows:

A Sm P = Green	*a Sm P* = Green
A Sm p = Green	*a Sm p* = Green
A sm P = Salmon	*a sm P* = Green
A sm p = Brown	*a sm p* = Green

LINKAGE RELATIONS OF *Y*, *Pl*, AND *Sm*

Preliminary tests of linkage of Pl and Sm

The first indication of the linkage of the *Sm* and *Pl* factors was observed in the progeny of an outcross of the original salmon with a purple plant having green silks. This plant proved to be heterozygous for both *Sm*

and *Pl*. To the distribution given on page 546 may be added the data from a duplicate planting by Dr. Emerson:

	Pl Sm	*Pl sm*	*pl Sm*	*pl sm*	Per cent of crossing-over
111–2	26	7	4	23	
From Emerson	25	9	4	38	
	51	16	8	61	17.6

Two other backcrosses were then made, which the following year gave the results:

	Pl Sm	*Pl sm*	*pl Sm*	*pl sm*	Per cent of crossing-over
238–9	76	24	20	93	20.3
241	60	4	4	66	6.3

Construction and results of three-point tests

In the meantime, crosses were made to involve the *Y* factor for yellow endosperm in addition to *Pl* and *Sm*, since *Y* and *Pl* were known to be linked. To get a satisfactory three-point backcross test involved several difficulties, as follows:

1. Yellow endosperm is not easily distinguished from white if brought in only by the pollen. This is assumed to be due to the dominant *Y*'s being represented only once in the triple-fusion endosperm nucleus. It is therefore desirable that the F_1 plants should be used as female parents in the backcrosses.

2. Brown silks are not readily separated from green. This difficulty can be avoided only by having red pericarp in each plant. But the presence of red pericarp obscures the color of the endosperm. So in order to make endosperm separations possible, the female parent of the backcross must be free from red pericarp.

3. Purple and dilute purple plants usually have some purplish pigment in the pericarp, which in some cases interferes with the classification of yellow endosperm.

4. The dominant *A* factor must be present in every individual where silk color separations are to be made.

5. Aleurone color must be avoided.

6. Presence of the dominant *B* factor, while not affecting accuracy, would nevertheless facilitate note-taking by making all the plants of two sharply differentiated classes, purple and sun red.

To avoid as many as possible of these difficulties and accomplish the results within the shortest period of years, the following procedure was put into effect: Crosses were made involving the factors *Y*, *Pl*, and *Sm* in different combinations. In all of these crosses, pericarp color and also the *R* factor for aleurone color were kept recessive. At the same time, an attempt was made to find or isolate a stock of the triple recessive of the desired composition. Tests of all available salmon-silk material revealed two closely related families breeding true for red pericarp, white endosperm, and recessive *r*. Both families consisted of sun red and dilute sun red plants showing the *B* factor to have been heterozygous. These were used the following year in the backcrosses. Their composition was *y y pl pl sm sm r r P P A A*, some plants being homozygous and some heterozygous for dominant *B*. Pollen of these plants was used on silks of the F_1 crosses.

These backcrosses were made in 1918 and the progenies were grown in 1919. The results are given in table 4 (page 550). The percentages of crossing-over are: *Y-Pl*, 28.9; *Pl-Sm*, 9.1; *Y-Sm*, 36.6; showing their relative order to be *Y-Pl-Sm*.

While material for these tests was being built up, some much less satisfactory backcrosses were made by pollinating white-endosperm, brown-silked, dilute sun red plants with pollen from crosses involving *Y*, *Pl*, and *Sm*. These were grown in 1918. The results are given in table 5 (page 551).

A summary of the percentages of crossing-over is given in table 6 (page 552).

The chromosome map

From the totals of all the data obtained on these linkage relations, the observed percentages of crossing-over are found to be 29.70 for *Y-Pl*, 10.01 for *Pl-Sm*, and 36.79 for *Y-Sm*. This shows their relative map order to be *Y-Pl-Sm*. The distance from *Y* to *Pl* as observed is 29.7,

TABLE 4. BACKCROSSES INVOLVING *Y*, *Pl*, AND *Sm*, 1919

Pedigree no.	Character of F_1	Non-crossovers		Crossovers *y-pl*		Crossovers *pl-sm*		Double crossovers	
		Y Pl Sm	*y pl sm*	*Y pl sm*	*y Pl Sm*	*Y Pl sm*	*y pl Sm*	*Y pl Sm*	*y Pl sm*
1451–3	*y pl sm* x *Y Pl Sm*	79	74	57	48	7	19	0	3
1454–6	*p yl mx s· Y Pl Sm*	32	24	20	16	1	4	0	1
		Y pl Sm	*y Pl sm*	*Y Pl sm*	*y pl Sm*	*Y pl sm*	*y Pl Sm*	*Y Pl Sm*	*y pl sm*
1457–9	*Y pl Sm* x *y Pl sm*	160	145	75	79	13	24	0	0
1460–2	*Y pl Sm* x *y Pl sm*	144	113	49	71	14	18	3	1
1463–6	*Y pl Sm* x *y Pl sm*	132	119	41	56	18	8	2	0
		Y Pl sm	*y pl Sm*	*Y pl Sm*	*y Pl sm*	*Y Pl Sm*	*y pl sm*	*Y pl sm*	*y Pl Sm*
1467–8	*y pl Sm* x *Y Pl sm*	72	67	16	20	2	10	0	0
1469–70	*y pl Sm* x *Y Pl sm*	124	99	39	36	10	10	0	0
1471–3	*y pl Sm* x *Y Pl sm*	109	99	52	68	16	10	0	1
		Y pl sm	*y Pl sm*	*Y Pl Sm*	*y pl sm*	*Y pl Sm*	*y Pl sm*	*Y Pl sm*	*y pl Sm*
1476–7	*Y pl sm* x *y Pl Sm*	43	45	23	13	13	5	1	0
1478–80	*Y pl sm* x *y Pl Sm*	69	83	25	26	11	21	1	0
1481–2	*Y pl sm* x *y Pl Sm*	58	50	18	24	15	11	4	4
Totals		1,940		872		260		21	

TABLE 5. BACKCROSSES INVOLVING *Y*, *Pl*, AND *Sm*, 1918

Pedigree no.	Character of F_1	Non-crossovers		Crossovers *Y-Pl*		Crossovers *Pl-Sm*		Double crossovers	
		Y pl sm	*y Pl Sm*	*Y Pl Sm*	*y pl sm*	*Y pl Sm*	*y Pl sm*	*Y Pl sm*	*y pl Sm*
772–3	*Y pl sm* x *y Pl Sm*	51	73	43	29	9	7	2	5
774–6	*Y pl sm* x *y Pl Sm*	63	94	50	40	13	8	4	1
781–2	*Y pl sm* x *y Pl Sm*	49	66	24	20	5	7	4	2
		Y Pl Sm	*y pl sm*	*Y pl sm*	*y Pl Sm*	*Y Pl sm*	*y pl Sm*	*Y pl Sm*	*y Pl sm*
777–8	*y pl sm* x *Y Pl Sm*	51	51	14	28	9	4	1	0
779–80	*Y Pl Sm* x *y pl sm*	29	31	18	12	4	4	4	1
Totals		558		278		70		24	

TABLE 6. SUMMARY OF LINKAGE DATA

Pedigree no.	Total number of plants	Percentage of crossing-over		
		Y-Pl	*Pl-Sm*	*Y-Sm*
111–2	136	.....	17.5	.....
238–9	213	.....	20.7	.....
241	134	.....	6.0	.....
Totals	483	.....	15.73	.....
772–3	219	36.1	10.5	40.2
774–6	273	34.8	9.5	40.7
781–2	177	28.2	10.2	31.6
777–8	158	27.2	8.9	34.8
779–80	103	34.0	12.6	36.9
Totals 1918	930	32.47	10.11	37.42
1451–3	287	37.7	10.1	45.6
1454–6	98	37.8	6.1	41.8
1457–9	496	31.0	7.5	38.5
1460–2	413	30.0	8.7	36.8
1463–6	376	26.3	7.4	32.7
1467–8	187	19.3	6.4	25.7
1469–70	318	23.6	6.3	29.9
1471–3	355	34.1	7.6	41.1
1476–7	143	25.9	13.3	37.8
1478–80	236	22.0	14.0	35.2
1481–2	184	27.2	18.5	37.0
Totals 1919	3,093	28.87	9.09	36.60
Totals 1918–1919	4,023	29.70	9.32	36.79
Totals of all data	4,506	.....	10.01	.....

or approximately 30 units. Since in such long distances double crossing-over may be expected, a corrected map distance should be 30 plus twice the per cent of unobserved double crossovers between the two points. But with the high amount of interference indicated by the small number of observed coincident crossovers in the two regions *Y-Pl* and *Pl-Sm*, the corrected value for these data is probably not much above 30 or 35. The value 10 for the map distance between *Pl* and *Sm* is probably correct for these data.

It should be understood that the chromosome map is primarily a graphic representation of the data on linkage relationships. Its correspondence with actual positions on the chromosome itself is not implied, tho the work of Morgan and his coworkers has given much evidence of at least a correspondence between relative map order and the actual relative position of the genes in the chromosome.

The variability of the percentages of crossing-over shown in table 6 is not greater than would be expected of heterogeneous data. Gowen (1919) has shown crossing-over in Drosophila to be an extremely variable phenomenon. Plough (1917) has shown it to be modified by temperature, and Bridges (1915) by age of the individual. The subject of variation of crossing-over in maize must remain for study with less difficult characters than those involved in these experiments.

The distributions when the F_1's were used as pistillate and as staminate parents give nearly the same averages, but the data are inadequate for any conclusion except that the crossing-over is not widely different in the two cases.

Coincidence of crossing-over

Coincidence of crossing-over in two regions of a chromosome is the ratio of observed coincident (simultaneous) crossing-over to the calculated expectancy. The expectancy is the product of the percentages of crossing-over of the two regions. The actual calculation may be simplified, as shown by Weinstein (1918). The derived formula is

$$\text{Coincidence} = \frac{xn}{ab}$$

in which n = the total number of individuals,

x = the number of coincident crossovers,

a and b = the total number of crossovers in the respective regions.

The coincidence of crossing-over in the two regions *Y-Pl* and *Pl-Sm*, calculated from tables 4 and 5, is as follows:

From table 4:

$$\text{Coincidence} = \frac{21 \times 3093}{893 \times 281} = 0.26$$

From table 5:

$$\text{Coincidence} = \frac{24 \times 930}{302 \times 94} = 0.79$$

From combined data of tables 4 and 5:

$$\text{Coincidence} = \frac{45 \times 4023}{1195 \times 375} = 0.40$$

These values are entirely comparable with those listed by Weinstein (1918) for Drosophila. From this and the similarity of all phases of linkage and crossing-over, it is evident that the mechanism of crossing-over in maize is not strikingly different from that in Drosophila except in one respect. In Drosophila, crossing-over occurs in oogenesis only, in spermatogenesis not at all. In maize the phenomena of crossing-over are at least of the same order in both megasporogenesis and microsporogenesis.

Summary of linkage studies

The factor *Sm* for salmon silk color is shown to be linked with the factor *Y* for yellow endosperm and the factor *Pl* for plant and anther color.

The relative order of these three factors is *Y-Pl-Sm*.

The amount of crossing-over between *Y* and *Pl* is about 30 per cent; between *Pl* and *Sm* it is about 10 per cent.

The observed coincidence of crossing-over in the two regions *Y-Pl* and *Pl-Sm* was about 0.4.

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17

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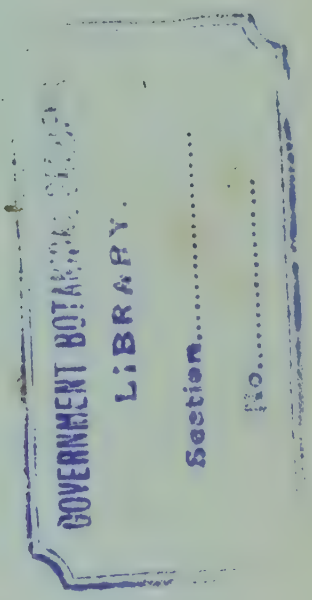
THE GENETICS OF SQUAREHEADEDNESS AND OF DENSITY IN WHEAT, AND THE RELATION OF THESE TO OTHER CHARACTERS

SARKIS BOSHNAKIAN



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CONTENTS

	PAGE
Physiological conditions affecting rachis internode length	802
Determination of density and of squareheadedness	803
Development of the wheat plant with reference to squareheadedness	804
The mechanics of squareheadedness	806
Effects of crossing on squareheadedness	807
Effects of nutrition	809
Summary	812
The genetics of squareheadedness	813
Inheritance of squareheadedness in crosses within the *sativum* group	814
Relation of the degree of squareheadedness of the *vulgare* parent in *vulgare* x squarehead crosses, to the squareheadedness of their progeny	824
False dominance of squareheadedness	826
Relation of width of culm to squareheadedness	827
Inheritance of squareheadedness in spelt x *sativum* crosses	829
Effect of the spelt factor on squareheadedness	831
Inheritance of squareheadedness in specific crosses	833
Summary	834
The genetics of density	835
Inheritance of density in crosses between *Triticum compactum* and other forms of the *sativum* group	836
Inflence of the density of the lax parent in a lax x *compactum* cross on the density of succeeding generations	843
Relation of density of F_2 plants to that of their progeny	844
Relation of density of dense and lax segregates of heterozygous F_2 plants	845
General consideration on the frequency distributions of compact x lax crosses	846
The nature of density factors	854
Factors producing squareheadedness as comprising one of the group of factors modifying degree of density	856
Relation of squareheadedness to density in F_2-generation plants	858
Relation of length of rachis to density in hybrid plants	865
Relation of length of culm to rachis length and density	866
Correlation between average internode length and length of sterile glumes	870
Correlation between average internode length and length of kernels	871
Relation of density of rachis to density of rachilla	872
The factor for spelting acting as a modifier for the density factor	874
The synthetic production of *Triticum compactum*	876
Summary	879
Literature cited	881

THE GENETICS OF SQUAREHEADEDNESS AND OF DENSITY IN WHEAT, AND THE RELATION OF THESE TO OTHER CHARACTERS

THE GENETICS OF SQUAREHEADEDNESS AND OF DENSITY IN WHEAT, AND THE RELATION OF THESE TO OTHER CHARACTERS[1]

SARKIS BOSHNAKIAN[2]

The mendelian inheritance of each of the more striking characters in wheat, such as beardedness, color, felting, density, and so forth, has been determined qualitatively by various workers. Much remains to be done, however, if the genetics of these characters is to be analyzed from a quantitative point of view, as there are numerous lesser inherited variations within their simple gross segregations.

Practically all of these characters show certain degrees and types of interrelations with other characters. Some of them show complete or partial linkage. Others, when analyzed quantitatively, appear to have been affected by one or another character but not necessarily linked with it, so that if one of these characters appears in an intense or a dilute form the others vary also in the same direction and more or less in the same degree.

Besides the above-mentioned type of interrelation, in which the appearance and the intensity of appearance of a group of characters are due to the presence or the absence of the same factor or factors, there is another type embracing a set of characters that appear as an indirect effect of the presence of another character. In a sense these characters are acquired, but they seem to be inherited simply because the causal character is inherited; and whenever the latter is present it gradually causes the modification of the former characters during the lifetime of the individual.

The subject of the inheritance of types of internode length presented in this paper has been treated from the following three viewpoints: (1) the analyses of minor segregations within gross (3:1, 1:2:1, or the like) segregations; (2) the determination of the interrelations of varied

[1] Paper No. 93, Department of Plant Breeding, Cornell University, Ithaca, New York. Also presented to the Faculty of the Graduate School of Cornell University, March, 1920, as a major thesis in partial fulfillment of the requirements for the degree of doctor of philosophy.

[2] In cooperation with the Office of Cereal Investigations, United States Department of Agriculture.

characters; and (3) the determination of characters that were found to be the resultant of other characters.

Since the characters studied were confined to those that were not distinctly contrasting in the usual mendelian sense but represented different gradations on a scale between two extreme quantitative characters, it was not possible to classify them into genetic classes or to express the results always in terms of ratios. The analyses were made according to such biometrical methods as seemed best suited to bring out the directions and tendencies of the variations. Factorial explanations, however, have been given wherever the facts obtained warranted the formulation of such hypotheses.

The material on which observations were made consisted, exclusive of interspecific crosses, of more than sixty F_2 progenies, fourteen of which were carried through the F_3. To avoid duplications of similar results it is not considered necessary to present here the results of all the crosses, but sufficient data are given to serve as illustrations and to show the general trend of the various modes of inheritance.

For many valuable suggestions and criticisms during the progress of this work the writer fully acknowledges his indebtedness to Professor H. H. Love, of the Department of Plant Breeding at Cornell University, under whose direction the studies were made. Most of the F_2 and F_3 progenies studied were furnished by Dr. C. E. Leighty, of the United States Department of Agriculture. The writer wishes to express his appreciation of Dr. Leighty's generosity in supplying these and also carefully numbered hybrid progenies, which made possible the tracing of each back to the F_1 and parental material, all of which had been saved. Thanks are due also to the Office of Cereal Investigations, United States Department of Agriculture, through whose courtesy the writer was enabled to enjoy the field and laboratory facilities at the Arlington Experimental Grounds during the summers of 1916 and 1917.

PHYSIOLOGICAL CONDITIONS AFFECTING RACHIS INTERNODE LENGTH

Like many quantitative characters, density and squareheadedness are affected to a greater or less extent by a number of environmental conditions which tend to change the normal course of development of the plant, thereby suppressing or accelerating the growth of certain of its

parts. A brief discussion of the effect of environmental factors on the production of these internode characters will serve to show to what extent nongenetic variations may take place. In the first part of this paper the main object is to explain the phenomena of density and squareheadedness on a purely mechanical basis.

DETERMINATION OF DENSITY AND OF SQUAREHEADEDNESS

The terms *density* and *squareheadedness* are used in this paper to designate two different phenomena of rachis internode length. The differences between these two characters are discussed elsewhere (Boshnakian, 1917)[3], but they may be briefly redescribed here.

Density is expressed in terms of average rachis internode length, which is found by dividing the length of the rachis by the number of rachis internodes. The average internode length, or density, of a head 90 millimeters long with 20 rachis internodes, is thus 90 ÷ 20, or 4.5 millimeters. The average internode length in wheat varies from about 1.3 to about 8 millimeters. In *vulgare* wheat it usually does not extend beyond 5 millimeters. Density is comparative.

The average internode length usually varies in dense wheats from 1.2 to 2.5 millimeters, and in lax forms from 3 to 5+ millimeters. There are intermediate gradations, but, in a general way, by *dense* or *lax* forms are meant, respectively, forms varying in density between the two ranges specified. Although the word *club* refers to a capitate type of head, following the present usage of this term it is here applied to dense wheats of the *sativum* group (that is, *Triticum compactum*) whether capitate or not.

Squareheadedness, on the other hand, refers to the ratio between the average internode length of the central third of the rachis and that of the terminal third. The density of the middle and upper thirds of the rachis is equal to the ratio of the number of internodes in these two sections of the rachis. The coefficient of squareheadedness is found by dividing the number of rachis internodes in the terminal third of the rachis by the number of internodes in the middle third. Thus, if the terminal third has 9.5 internodes and the central third has 5.6 internodes, the degree of squareheadedness is equal to 9.5 ÷ 5.6, or 1.69. The forms

[3] Dates in parenthesis refer to *Literature Cited*, page 881.

that are usually called *squareheads* have a coefficient of about 1.33 or more; and in this paper, by *vulgare* or *non-squarehead* forms are meant types with coefficients of less than 1.33, and by *squareheads*, forms having coefficients of more than 1.33. This division is entirely arbitrary and is made for convenience.

It is seen, then, that squareheadedness has no reference to density. Squareheads may be dense or lax. This divides the wheat types into the following four classes with respect to their rachis internodes: non-squarehead, lax (*Triticum vulgare*, Plate LXVII, upper, 12); squarehead, lax (*Tr. capitatum*, Plate LXVII, upper, 11); non-squarehead, club (*Tr. compactum*, Plate LXVII, lower, 13); squarehead, club (*Tr. compacto-capitatum* Plate LXVII, upper, 9). These varietal names apply to the wheats of the *sativum* group only.

According to these classifications, the semi-dense forms having a squareheadedness of less than 1.33 are named *semi-dense vulgare*—not *squareheads*, a name too often applied for such forms, and perhaps with some justification as such semi-dense forms when well developed may appear square in cross section.

Since the discussions in this paper center solely upon squareheadedness and density, it is necessary for the reader to bear in mind the sense in which these two terms are used.

DEVELOPMENT OF THE WHEAT PLANT WITH REFERENCE TO SQUAREHEADEDNESS

The head of the wheat plant is found in an embryonic stage when the plant starts a new growth after a short or a long period of rest. When the head is about 10 millimeters long it is covered with concentric rings of sheaths, each sheath being attached to the culm at its respective node. The different parts of the plant do not all grow at the same rate.

When the spike is about 15 millimeters long, the enveloping sheaths and blades are fairly well developed, but the culm internodes are only a few millimeters in length, the terminal ones being the shortest. After the sheaths have gone through their chief period of growth, the development of the internodes is accelerated. During this period the head also begins to develop. From this time on, the increase in the height of the

VARIOUS FORMS OF GROWTH

Upper: 1, *Aegilops ovata*. 2, F1 (Aegilops x Silver Club); 3, Silver Club. 4, White Spelt; 5, Dale Gloria; 6 to 12, F2 types (White Spelt x Dale Gloria, series 13255a) — 6, homozygous lax spelt; 7, heterozygous dense spelt; 8, homozygous dense spelt; 9, homozygous dense *sativum* club; 10, heterozygous dense *sativum*; 11, homozygous lax *sativum*, squarehead; 12, homozygous lax *sativum, vulgare*

Lower: Dense forms of different species: 1, *durum*; 2 and 3, capitate and dense barley heads (lateral florets of 2 removed); 4, capitate *sativum*; 5, dense spelt; 6, dense *polonicum*; 7 and 8, club wheats; 9, *turgidum*; 10, club; 11 and 12, capitate *dicoccums*; 13, club pyramidal; 14, capitate spelt; 15, dense *polonicum*; 16, club

VARIOUS FORMS OF GROWTH

Upper: 1 to 5, 6 to 10. Heads of two hybrid plants showing lack of harmony of growth characters. 11 and 12. Heads of spelts subjected to longitudinal pressure; zigzagging of internodes produced instead of squareheadedness.

Lower: 1 to 4, 5 to 8. Heads of two plants showing variations in density on same plant; plants grown in greenhouse; long spikes headed out about four weeks earlier than dense spikes.

plant is due primarily to the increasing length of each culm internode. During the first period of the development of the culm, the basal internodes, except a few near the ground, begin to develop, and successive internodes undergo their chief period of growth as the growth of the internode below is beginning to decline. The terminal section of the culm, which carries the spike, during its development has to push the spike up all along the length of the terminal sheath, which envelops the head in such a way that occasionally, and especially among plants of hybrid origin, the culm cannot exert sufficient pressure to unfold the sheath. In such cases the spike fails to head out; or, if it finally does head out, the head appears in an abnormal condition and the tip spikelets very often remain undeveloped (Plate LXVIII, upper, 1 to 10).

The factors that seem to produce a strain on the terminal culm internode during its growth are the following: the rapid growth of the culm; the spread, width, shape, and texture of the spikelets; the stiffness of the enveloping sheath and its resistance to unfolding.

It seems that as the rate of growth of the terminal culm increases, the movement of the spike through the sheath should encounter a greater degree of resistance in an opposite direction.

The spread of the spikelets is probably one of the most important factors. The glumes of the spikelets are pointed upward and outward. This in itself tends to increase resistance. If the contact of the glumes with the sheath increases their spread, the resistance will increase many fold. In species such as the spelt or the emmer, in which the spikes are very narrow and the spikelets are very close to the rachis, the resistance is decidedly decreased because the spikelets themselves assume a wedge shape, the glumes being drawn together tightly; and also because the spikelets, lying flat against the rachis, are not likely to spread out.

The third factor, which is not so important as the other two, is the texture of the sheath and its habit of development. The sheath that normally unfolds at the proper time, or is easily unfolded by the movement of the spike, sometimes fails to open completely or opens under difficulty. Sheaths of this type produce a considerable longitudinal pressure on the culm.

THE MECHANICS OF SQUAREHEADEDNESS

In order to understand the mechanics of the production of squareheadedness, it is necessary to know the effect that is produced by pressure along the culm axis. The presence of longitudinal pressure is evident from the undulations of the culms often observed in square or dense forms (Plate LXVII, lower, 9 and 16.) The part of the spike that most reacts to the effect of pressure is the terminal part, because it is directly in contact with the sheath. The pressure produces a compressing effect, and this in turn checks the development of the terminal part of the head, especially the development of the rachis internodes, and produces the effect known as squareheadedness.

This character of squareheadedness is mainly evidenced by the gradual shortening of the terminal rachis internodes (Plate LXVII, lower, 4, 11, and 12). But there are also other characters which accompany this shortening of the internodes and which are the direct or indirect results of the same cause. One of the most prominent of these is the so-called clubbing, or capitate form, produced by the spreading of the spikelets away from the rachis in those regions of the head where the internodes are short. Because of the pressure exerted, the normal elongation of the internodes is inhibited but the spikelets in most cases continue to develop. Since the space between the spikelets is not sufficient, they are forced mechanically to spread out to make more room for development. This process is on the principle of the isosceles trapezoid, in which, the base being constant, the distance between the sides increases as the latter take a position toward a right angle with the base. In the plant the rachis internode is represented by the base, and the axes of the spikelets by the sides, of the trapezoid.

In squareheads the spikelets of only the upper part of the spike (except the terminal two or three spikelets) thus diverge. In most *compactum* forms all spikelets diverge as a result of the shortness of all the internodes. This is seen on comparing the divergence of spikelets of dense heads 5 and 9, in Plate LXVII (upper), with that of lax heads 2, 4, and 6. In wheat, as well as in barley, the opposite condition exists also in some cases; that is, the shortening of the internodes does not occur near the upper part, but near the basal region. In such cases the ear, in-

stead of being capitate in form, assumes a pyramidal or conical form, as shown by heads 13, Plate LXVII (lower), and 8, Plate LXVII (upper).

Another phenomenon of squareheadedness is the drawing of the terminal spikelets toward one side so that when the head is viewed along one of the directions of the plane of symmetry, which separates the spikelets of one side from those of the other, the rachis appears exposed (Plate LXVII, upper, 11). Viewed from the opposite side the rachis is covered by glumes and awns which are outdrawn and gathered in that direction. With the receding of the glumes the part of the side where the rachis is exposed appears flat (Plate LXVII, upper, 11), and to a person not viewing the head from the opposite side also it gives the impression that the spike is square in cross section. This impression, which has been left on the popular mind, has given to this form the name *squarehead.*

The character of squareheadedness is not confined to the wheat known by this name but may appear also in the dense forms known as club wheats (*Triticum compactum*). The total shortening of rachis internodes in these forms is primarily due to the presence of a genetic factor which produces also a general shortening of many parts of the plant. But in most forms a certain degree of squareheadedness may be found. This may be inherent—that is, transmissible—or it may have been produced mechanically. When the spikelets spread out as a result of the shortness of the internodes, as described above, the increased width of the head and the projections of the tips of the glumes are likely to offer considerable resistance, thus producing squareheadedness in the manner already explained.

EFFECTS OF CROSSING ON SQUAREHEADEDNESS

Squareheadedness, and shortening of all the rachis internodes, are two different phenomena. As shown in the preceding discussion, squareheadedness is a postnatal character, as it were, being dependent on the combined effect of certain vegetative growth characters. Density of the *compactum* wheats, on the other hand, is predetermined and is due to the presence of one or more genetic factors which cause dwarfing of a number of plant parts, including incidentally the shortening of all rachis internodes.

Squareheadedness is dependent on a certain balance of the rate of

growth of the parts concerned. An unfavorable balance produced through hybridization may result in certain hereditary anomalies. A few such forms are shown in Plate LXVIII (upper). Heads 1 to 5 were produced on a single F_2 plant derived from a cross between a *durum* and a common wheat. In these cases the curling of the awns all along the length of the heads shows that the latter were partly prevented from moving up the sheaths by the tightening of the sheaths. The illustrations show also the rudimentary condition of the terminal 5 to 7 spikelets, which represent the region whose growth was checked altogether by being subjected to pressure.

Heads 6 to 10 in the same plate represent another condition of lack of harmony of growth between different parts of the plant. The spiral form of the awns of head 7 shows that this head was forced to make a corkscrew movement while making its way up the sheath. Heads 8 and 10 show the failure of the sheath to open at the proper time. Heads 6 and 9 represent heads that were finally released.

Heads 11 and 12 represent a single spelt plant whose sheaths were evidently wrapped too tightly around the heads. The pressure which the tight sheath exerted on the head by the growth of the culm produced a zigzagging of the rachis. The internodes of the spelts, being comparatively stiff, are not so likely to remain short as a result of pressure.

These two spelt heads are interesting because they show the relative tendency of the different internodes to be affected by pressure. The basal internodes are thick and are very slightly affected by the induced zigzagging effect. Each successive internode is weaker than the one below, and more and more likely to show the effect of pressure. The conditions to which these heads were subjected are identical with those to which squareheads of *sativum* or other soft-glumed species are subjected, but the effect is somewhat different because of the differences of texture and ear form of the spelt as compared with those of some other forms.

These cases show that there are a number of growth characters to which the production of squareheadedness is due, and that the factors producing these characters seem to segregate and recombine like any other factors. If the combination is such as will produce a pressure of

the head in a certain rate and intensity, various degrees of squareheadedness may result. If the head encounters little or no pressure the internodes may be more or less uniform, and if the growth of parts is unbalanced certain abnormalities of the spike may result.

Since a number of morphological factors are concerned in the production of squareheadedness, logically it would be expected, and experimentally it would be found, that the segregates of a cross between a squarehead and a non-squarehead do not appear in a definite ratio but give a distribution approaching the normal curve of error.

EFFECTS OF NUTRITION

In one of the preliminary experiments to determine the effect of nutrition under field conditions, seeds from a pure variety of a squarehead were grown at varying distances. In one case the seeds were drilled rather closely; in the second case they were planted 7.5 centimeters apart; in the third case they were planted 15 centimeters apart. The frequency distribution of squareheadedness of these three sets of plantings is given in table 1. The set that was drilled in had a mean degree of squareheadedness of 1.325 ± 0.012; the seeds planted 7.5 centimeters

TABLE 1. VARIATIONS OF SQUAREHEADEDNESS IN PLANTS GROWN AT VARYING DISTANCES
(Variety, Giant Squarehead)

	Squareheadedness													Number of plants	Mean
	1.00	1.10	1.20	1.30	1.40	1.50	1.60	1.70	1.80	1.90	2.00	2.10	2.20		
Seeds drilled	1	14	18	25	19	3	10	2	..	2	..	..	..	94	1.325±.012
Seeds planted 7.5 cm. apart	..	..	1	..	8	3	10	7	3	3	2	4	1	42	1.678±.025
Seeds planted 15 cm. apart	..	2	6	..	2	..	1	..	..	..	..	..	..	11	1.254±.027

apart gave a higher mean, 1.678 ± 0.025; and those planted 15 centimeters apart gave a mean of but 1.254 ± 0.027.

The plants from the drilled rows made a fair growth but were inferior to those of the second set. The plants of the third set were mostly winterkilled, and such as survived had a poor stand with heads of varying length and degrees of development. The poor condition of the last-named was due to the wide distances between the plants, which made them unable to protect themselves from winter conditions. In the case of the other sets there was enough foliage developed during the fall for winter protection.

Disregarding the third set, it is apparent that the high degree of squareheadedness of the second set was due to the greater feeding allotted to these plants; for there was also a corresponding general development.

Another experiment was made with potted plants growing under greenhouse conditions. It consisted of four sets of nine pots. One set was grown in a cool house, the second under moderate greenhouse conditions, the third in a damp chamber, and the fourth in a rather warm place. Each set consisted of triplicate pots containing, respectively, soils of a very poor sandy mixture, of fair fertility, and of higher fertility.

In the sets grown in cool and moderate temperature conditions, the pots containing poor soil produced heads of a low degree of squareheadedness, while the heads of plants grown in moderately fertile soils showed a higher degree of squareheadedness.[4]

There is no question that in these cases the high degree of squareheadedness was produced by the fertility of the soil. That fertility increases squareheadedness has been noted by Edler (1903), Preul (1908), Ohlmer (1908), and Meyer (1909). Meyer found in addition that nitrogen was the causative factor, as neither calcium, potassium, nor phosphorus, alone or in combination, had any noticeable effect on the production of this character.

It is not so difficult to explain how high fertility increases squareheadedness, in the light of the causes of squareheadedness given in the preceding discussions. If rapid growth of the culm subjects the head to higher pressure, the spike takes the squarehead form. By increasing the nitrogen content of the soil, the rate of growth of the culm is accelerated and the tissues of the parts of the head are softened. The first of these conditions increases the pressure to which the head is subjected, and the second renders the head more sensitive to the effect of pressure. In the absence of sufficient nitrogenous food, the rate of growth is retarded and the parts of the head become fibrous. Due to the first condition sufficient pressure is not developed, and with the hardening of the tissues the spike offers a greater resistance to whatever pressure may be developed.

[4] The sets grown in the damp chamber and in the warm place did not do well.

The effect of the rate of growth on squareheadedness may be determined also by ascertaining the degree of squareheadedness of the leading culm and of those that develop later. Practically in every case the leader, which is by far the most vigorously growing culm, has a higher degree of squareheadedness than the others. Often the smaller culms of squarehead plants will have *vulgare*-like heads.

In cases in which squareheading is increased by the rapid growth of the culm, the plants having longer spikes are more squareheaded than those with shorter spikes. The relative degree of squareheadedness of short and of long spikes of the same plant is shown in table 2. From four to six well-developed heads were measured from each plant in connection with another experiment. Here the shortest and the longest of these, respectively, are shown. Out of twelve cases taken at random there was but one case in which the short head had a higher degree of squareheadedness. The average of the summation of the differences was 0. 17 ± 0.021 in favor of the long heads.

TABLE 2. DIFFERENCES IN DEGREE OF SQUAREHEADEDNESS OF LONG AND OF SHORT HEADS OF THE SAME PLANT

Short heads		Long heads		
Length (centimeters)	Squareheadedness	Length (centimeters)	Squareheadedness	Difference in squareheadedness
10.0	1.23	13.5	1.47	+0.24
11.6	1.41	13.2	1.51	+0.10
10.4	1.50	13.8	1.50	0.00
10.3	1.24	12.0	1.51	+0.27
10.7	1.21	14.0	1.37	+0.16
10.5	1.24	13.6	1.48	+0.24
8.0	1.39	10.5	1.60	+0.21
7.6	1.31	10.0	1.65	+0.34
8.7	1.51	10.1	1.65	+0.14
8.4	1.33	11.2	1.57	+0.24
8.3	1.39	12.5	1.58	+0.19
7.9	1.29	10.3	1.17	−0.12
Mean and average error				
9.4±.35	1.34±.025	12.0±.40	1.50±.026	+0.17±.021

When vigor is induced by soil fertility, the plants with longer heads will be more squareheaded than the others; and when vigor is induced by crossing certain *vulgare* forms, the long heads of each plant will be found to be more of a squareheaded type. The increase of squareheadedness of the F_1 plants, as shown later, will serve as examples.

If, on the other hand, squareheadedness is caused, not so much by the

vigorous development of the culm, but by the failure of the sheath to unfold at the proper time, then the plants that are more squareheaded will be found to have shorter heads that the non-squarehead forms. Figures illustrating this type of squareheadedness are given in connection with the discussion of that subject.

Before concluding the discussion of the effects of nutrition, it may be well to make a few remarks regarding its effect on the density of the *compactum* form. As already mentioned, the density of this form is not the result of pressure. But by increasing the fertility of the soil it is possible to change markedly the degree of density. Four heads from each of two *compactum* plants are shown in Plate LXVIII (lower). These two plants were grown in 4-inch pots in a greenhouse. The soil was highly fertilized. The heads first developed (2, 4, and 5) were almost like *vulgare*, but as the season advanced, and more spikes began to head out, the heads became more and more dense. There was an interval of about four weeks between the time of heading-out of the first and of the last head. When the last spike headed out, the first one was almost ripe—that is to say, the nutrients in the plant or those in the soil were already used up; hence the spikes heading out later obtained very little food. From the difference in thickness of the culms of dense and lax heads an idea may be formed of the relative amount of nourishment obtained by the different heads.

This experiment was conducted under abnormal environmental conditions, and it is not likely that variations as great as these will be found on plants growing under field conditions. But it points out the fact that increased fertility in the soil tends to increase the length of the rachis internodes.

SUMMARY

The wheat plant during its development undergoes two more or less distinct periods of growth. In the first period the sheaths and the blades develop. In the second period the rate of growth of the sheaths diminishes and the culms begin to develop, and during this period the spike carried at the end of the terminal culm internode is pushed up through the enveloping sheath.

Squareheadedness is the combination of a number of characters which

are produced by the shortening of the terminal rachis internodes. It is expressed by the coefficient found by dividing the number of internodes in the terminal third of the rachis by the number of internodes in the central third.

Density is the shortening of all the rachis internodes. It is determined by dividing the length of the rachis in millimeters by the number of internodes.

There are numerous gradations of squareheadedness and of density.

Squareheadedness is the result of pressure developed by differential growth of culm and sheath.

Rapid growth of the culm, failure of the sheath to unfold, and ears with soft-spreading glumes, tend to increase squareheadedness.

Any factor, genetic or environmental, which affects principally the development of the above-named characters, will affect the degree of squareheadedness.

Fertility of the soil or access of the root system to sufficient available nitrogenous matter increases squareheadedness.

Density is purely an inherited character, but favorable growth conditions may somewhat increase average internode length. Under abnormally favorable or unfavorable conditions, the increase or the decrease of density even on the same plant may be considerable.

THE GENETICS OF SQUAREHEADEDNESS

Investigations on the genetics of squareheadedness have given many confusing results, chiefly because no definite standards have been used for measuring this character. There are many instances in which this word has been used for designating a moderate degree of density.

One of the earliest studies of the subject was made by Rimpau (1891), who crossed lax *vulgare* types with lax and moderately dense squareheads. The F_1 hybrids were intermediate and the types of the F_2 populations varied within respective parental ranges.

Von Rümker (1909) obtained from squarehead x *vulgare* crosses, F_2 populations, some of which yielded more and others fewer squareheads. The squareheads varied also in degree.

Nilsson-Ehle (1911) found the *vulgare* type to be dominant over the

squarehead form. The ratio of *vulgare* to squarehead was between 3:1 and 15:1.

Further work has been done, but because of the different meanings given to the word *squarehead* it is not possible to compare the results with those that are here presented.

INHERITANCE OF SQUAREHEADEDNESS IN CROSSES WITHIN THE SATIVUM GROUP

Squareheadedness is a quantitative character. Crosses in which it is involved do not show a clear-cut segregation into mendelian classes and ratios. Physiological experiments have shown that the character is the result of the interaction of a number of growth factors, certain combinations of which cause the compacting of the terminal part of the spike. The character is very variable, for any environmental condition that affects these growth factors in one way or the other indirectly increases or decreases the degree of compactness of the terminal part of the rachis.

Before considering the inheritance of the character in squarehead x non-squarehead crosses, it may be well to illustrate the mode of inheri-

TABLE 3. DEGREE OF SQUAREHEADEDNESS IN VULGARE x VULGARE CROSSES

	Generation	Degree of squareheadedness																Mean	Number of plants
		0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	
Parent plants																			
Mealy	...	..	..	1	2	6	2	7	4	4	1	1	..	..	..	..	..	..	1.14	28
Jones Longberry	...	..	..	..	1	2	6	3	2	1	..	..	..	..	..	..	..	..	1.12	15
Pride of Genesee	...	..	1	3	4	2	4	6	1	1	1	..	..	..	..	..	..	..	1.08	23
Dawson Golden Chaff	...	2	1	6	6	2	..	..	..	..	..	..	..	..	..	..	..	..	0.98	17
Crosses																			
13158a Mealy x Jones Longberry	F_1	..	..	..	..	..	..	..	..	..	3	1	1	1	..	..	..	..	1.35	6
13158a Mealy x Jones Longberry	F_2	..	..	2	7	13	14	9	5	6	4	1	..	..	..	..	..	..	1.12	61
13178a Jones Longberry x Mealy	F_1	..	..	..	..	..	..	..	..	1	..	..	..	..	2	1	2	..	1.50	6
13178a Jones Longberry x Mealy	F_2	1	..	3	3	8	9	5	6	4	9	2	3	1	..	..	..	1	1.17	55
13179a Jones Longberry x Mealy	F_1	..	..	..	..	..	..	..	..	..	..	1	..	2	..	..	..	..	1.42	3
13179a Jones Longberry x Mealy	F_2	1	4	3	13	17	15	17	10	4	4	2	..	..	..	..	..	..	1.11	90
13177a Dawson Golden Chaff x Pride of Genesee	F_1	..	..	..	1	1	3	2	..	..	..	..	..	..	..	..	..	..	1.09	7
13177a Dawson Golden Chaff x Pride of Genesee	F_2	..	1	5	25	14	9	6	6	2	1	1	..	..	..	..	..	..	1.06	70

tance of squareheadedness when either the squareheads or the *vulgare* type (non-squareheads) are crossed among themselves.

The degree of squareheadedness in F_1 and F_2 generations of *vulgare* x *vulgare* crosses is shown in table 3. The first three crosses here (series 13158a, 13178a, and 13179a) are between Mealy and Jones Longberry, both of which have practically the same degree of squareheadedness, 1.14 and 1.12, respectively. The mean degree of squareheadedness of the F_2 generation fluctuated around the means of their parental forms, being, respectively, 1.12, 1.17, and 1.11.

The fourth cross, 13177a, was made between plants of lower coefficient; that of Pride of Genesee was 1.08 and that of Dawson Golden Chaff was 0.98. The F_2 generation from this cross were all non-squareheads and had a mean squareheadedness of 1.06, these also somewhat approaching the average of their parents.

The degree of squareheadedness in crosses between squareheads is shown in table 4. The F_2 of the first cross, 13201a, has a range with-

TABLE 4. DEGREE OF SQUAREHEADEDNESS IN SQUAREHEAD X SQUAREHEAD CROSSES

	Generation	Degree of squareheadedness																				Mean	Number of plants
		1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85	1.90	1.95	2.00	2.05	2.10	
Parent plants																							
New Soules	..	..	..	..	..	..	..	..	..	2	..	3	..	3	2	2	1	2	..	..	..	..	1.71	15
Giant Squarehead	..	..	..	..	..	..	2	..	1	..	3	1	1	5	4	4	1	4	1	3	2	1	1.77	33
Jones Mammoth Amber	..	..	..	..	..	2	..	2	2	2	4	2	..	1	..	..	..	..	..	..	..	..	1.49	15
Crosses																							
13201a New Soules x Giant Squarehead	F_1	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	2	1	..	..	..	1.87	5
13201a New Soules x Giant Squarehead	F_2	1	..	2	4	4	11	8	12	7	10	2	2	6	1	2	..	..	..	..	..	..	1.46	72
13203a Jones Mammoth Amber x Giant Squarehead	F_1	..	..	..	..	..	..	1	..	..	..	1	..	1	..	..	..	..	..	..	..	..	1.55	3
13203a Jones Mammoth Amber x Giant Squarehead	F_2	..	..	..	2	1	7	4	7	6	4	5	7	3	2	2	..	.	1	..	1	..	1.53	52

in the squarehead classes with a mean of 1.46. Compared with the averages of the parental forms—New Soules, 1.71, and Giant Squarehead, 1.77—the mean of the F_2 is lower. The second cross, 13203a, has an F_2 mean squareheadedness within the means of the parents.

There are two points of interest in connection with these two sets of crosses: first, as a rule, when *vulgare* forms are crossed among themselves or squareheads are crossed among themselves, the F_2 generation

TABLE 5. DEGREE OF SQUAREHEADEDNESS IN SQUAREHEAD x VULGARE CROSSES

	Generation	Degree of squareheadedness																													Mean	Number of plants
		0 75	0 80	0 85	0 90	0 95	1 00	1 05	1 10	1 15	1 20	1 25	1 30	1 35	1 40	1 45	1 50	1 55	1 60	1 65	1 70	1 75	1 80	1 85	1 90	1 95	2 00	2 05	2 10			
Parent plants																																
Giant Squarehead														2		1		3	1	1	5	4	4	1	4	1	3	2	1	1.77	33
New Soules																	2		3		3	2	2	1	2					1.71	15
Extra Early Windsor													1		6	3	4	4	1	1	2	1		1						1.57	24
Jones Mammoth Amber												2		2	2	2	4	2		1										1 49	15
Minnesota 169						1	2	6	8	8	8	5	1	2																1.15	41
Mealy						1	2	6	2	7	4	4	1	1																1.14	28
Fultz					1	3	1	3	3	2																				1.04	13
Fultzo-Medit								5	1	5	2																			1.12	13
Pride of Genesee					1	3	4	2	4	6	1	1	1																	1.08	23
Jones Longberry							1	2	6	3	2	1																		1.12	15
Rural New Yorker							1	6	2	2	1																			1.08	12
Crosses																																
13131a Giant Squarehead x Minn. 169	F1													1																1 35	1
Ditto	F2						11	11	11	17	21	18	17	4	8	5	3	1	1	4		1	1		1					1.24	135
13150a Minn. 169 x Giant Squarehead	F1													2		1	1													1.41	4
Ditto	F2						3	3	3	5	7	18	9	6	3	5	4	2	1	2	3					1				1.31	75
13156a Minn. 169 x Giant Squarehead	F1											1		1			2													1.40	4
Ditto	F2							4	6	6	9	4	8	8	9	5	2	5	4	1	1	1	1							1.33	74
13134a Giant Squarehead x Mealy	F1																		1	1										1 62	2
Ditto	F2				1	2	6	4	11	9	7	11	9	8	7	2	2	3	6		4	3								1.29	95
13135a Giant Squarehead x Mealy	F1															1		1	2	1										1.62	5
Ditto	F2			1	2	1	2	6	1	7	11	11	11	12	9	11	12	8	5	2	4		1	2	1	1				1.36	121
13137a Giant Squarehead x Fultz	F1															1	1		1											1.51	3
Ditto	F2	1			4	8	14	13	9	8	11	6	5	7	4	4	3	6	2	2	1		2	1						1.21	111
13138a Fultz x Giant Squarehead	F1												1		1		1	1	1											1.47	5
Ditto	F2		1		1	2	8	13	11	4	8	7	7	8	3	6	1	1	1	2	1	4								1.22	89
13140a Giant Squarehead x Fultzo-Mediterranean	F1																					1	1							1.77	2
Ditto	F2						1	2	3	3	6	10	8	14	12	10	9	7	7	4	1	2	1				1			1.40	101
13141a Giant Sq. x Pride of Genesee	F1															1		1		1										1.55	3
Ditto	F2						4	8	10	10	6	13	5	1	7	2	2	1	1			1								1.22	71
13200a Pride of Genesee x Giant Squarehead	F1	Not recorded																														
Ditto	F2		1		1		3	7	5	7	8	10	7	6	3	6	4		3		1	1	2		1					1 28	76
13202a Jones Longberry x Giant Sq.	F1																			2	2									1.68	4
Ditto	F2						1	4	4	6	2	9	8	6	7	12	4	2	2	4	1	1		1						1.80	74
13194a Pride of Genesee x New Soules	F1															3		1	1	1										1.52	6
Ditto	F2						4	3	6	9	10	11	4	7	3	2	1	4		1										1 24	65
13144a New Soules x Pride of Genesee	F1																					1								1.75	1
Ditto	F2					1	6	10	4	9	5	13	3	4	3	10	2	1	2	1	1			1						1 25	76
13176a New Soules x Rural New Yorker	F1													2			1													1.40	3
Ditto	F2			1			4	4	13	5	13	9	11	7	7	3	5	1	2											1 25	85
13196a Pride of Genesee x Extra Early Windsor	F1														2		1	1												1.46	4
Ditto	F2						3	2	6	8	14	11	12	10	6			1												1 24	73
13193a Jones Mammoth Amber x Mealy	F1														1	1														1 42	2
Ditto	F2					3	4	13	14	14	9	7	8	7	3	4	3	2	2	1		1								1 22	95
13143a Extra Early Windsor x Pride of Genesee	F1	Not recorded																														
Ditto	F2						1	4	3	10	7	12	8	4	5	5	2		1	1	1									1.27	64

consists of practically only *vulgare* or only squareheads, respectively; secondly, the mean of the F_2 generation approaches the average of the parental forms.

Regarding the inheritance of squareheadedness among squarehead x *vulgare* crosses, an idea can be obtained by comparing the F_2-generation distributions with the parental distribution (table 5). Special attention might be called to the comparatively high degree of squareheadedness of the F_1 generations; in most of the cases the F_1 plants are almost as squareheaded as the squarehead parents. On a theoretical basis the means of the F_1 would be expected to coincide with those of the F_2. The departure here is too wide. This increase in squareheadedness of the F_2 is attributed both to heterosis and to greater care taken in growing and spacing the plants of this generation.

The F_2-generation distribution, even when the number of individuals of which they are composed is considered, shows certain characteristics with respect to range of distribution and mean. If the F_2 distributions of squarehead and non-squarehead crosses are compared with those of the crosses in which the parents were either both squareheads or both *vulgare,* it is seen that so far as the mode of inheritance is concerned there is no essential difference between them. The means of the F_2-generation plants shift toward or away from the more squarehead classes, but show a constant tendency to regress toward the means of the parental forms; and the range of the F_2 also spreads or contracts, depending on the extent to which the parents vary in degree of squareheadedness.

Although several of these crosses were carried through the F_3 generation because of the similarities of the results, only two series are considered here to illustrate the behavior of the F_2 plants in F_3. The results of Giant Squarehead x Fultzo-Mediterranean (series 13140a) are shown in table 6, and those of Giant Squarehead x Mealy (series 13135a) are shown in table 7.

TABLE 6. BEHAVIOR OF SQUAREHEADEDNESS OF F_2 PLANTS IN F_3. SERIES 13140a, GIANT SQUAREHEAD X FULTZO-MEDITERRANEAN

	Degree of squareheadedness																													Mean	Number of plants
	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85	1.90	1.95	2.00	2.05	2.10	2.15	2.20		
P_1 Giant Squarehead	..	..	..	..	..	..	..	..	..	2	..	1	..	3	1	1	5	4	4	1	4	1	3	2	1	..	..	1.77	33
P_1 Fultzo-Mediterranean	..	..	..	5	1	4	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.12	13
F_1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	1.77	2
F_2	..	..	1	2	3	3	6	10	8	14	12	10	9	7	7	4	1	2	1	..	..	..	1	..	..	..	..	..	1.40	101
F_3 families																															
Pedigree	Squareheadedness in F_2																														
24-1	1.36	1	1	3	6	4	7	4	3	3	3	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.16	37
24-2	1.61	..	..	1	3	2	4	4	3	4	5	1	3	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	1.27	32
24-3	1.33	..	..	1	6	..	4	5	3	3	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.17	23
24-4	1.28	..	..	2	3	1	2	12	12	2	3	3	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.23	42
24-5	1.54	..	..	..	1	1	2	3	2	4	3	4	2	..	1	..	1	..	1	..	..	..	..	..	..	..	..	..	..	..	1.33	25
24-6	1.62	..	..	1	3	2	9	2	6	7	1	3	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.22	35
24-7	1.53	..	..	1	2	2	4	6	1	2	1	1	1	3	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	1.30	25
24-8	1.17	1	1	3	6	9	5	1	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.10	30
24-9	1.59	..	..	..	1	1	1	2	4	1	1	2	4	2	2	1	1	..	1	..	..	..	..	..	..	..	..	..	..	1.38	24
24-10	1.45	..	..	2	2	2	2	3	6	6	4	6	2	3	2	3	..	..	..	..	1	..	..	..	..	..	..	..	..	1.33	44
24-11	1.34	..	..	1	3	2	10	6	3	1	2	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.18	29
24-12	1.64	..	..	1	..	1	1	..	3	3	5	2	4	3	4	1	3	5	2	..	..	..	..	1	..	..	..	..	..	1.47	39
25-1	1.36	..	..	2	3	4	4	4	4	4	1	..	3	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	1.22	30
25-2	1.37	1	..	..	1	2	2	..	1	..	..	2	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	1.23	10
25-3	1.01	1	6	14	7	8	..	2	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.04	39
25-4	1.21	2	1	6	8	9	3	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.05	30
25-5	1.52	..	..	..	2	3	5	3	10	8	1	2	1	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.27	40
26-1	1.28	..	..	1	3	3	4	6	5	4	4	4	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.25	37
26-2	1.37	..	..	1	..	3	4	6	4	3	1	6	4	4	5	2	..	..	..	..	..	..	..	..	..	..	..	..	..	1.34	43
26-3	1.42	..	..	..	..	..	2	1	1	1	2	2	1	2	1	2	2	1	..	..	..	..	..	..	..	..	..	..	..	1.43	18
26-4	1.40	..	1	..	..	..	1	5	..	6	5	4	1	2	2	3	1	..	1	1	..	..	..	..	..	..	..	..	..	1.39	33
26-5	1.50	..	..	1	..	3	1	1	..	4	3	2	1	1	4	1	4	1	..	1	..	..	..	..	..	..	..	..	..	1.42	28
26-6	1.52	..	..	..	5	3	9	4	9	8	3	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.22	43
26-10	1.48	..	1	1	1	3	8	4	2	2	2	1	2	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.22	29
26-11	1.57	..	..	1	7	2	7	4	5	2	1	1	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.19	33
26-12	1.45	..	..	1	1	1	2	..	7	9	2	2	5	3	2	3	..	..	1	..	..	..	..	..	..	..	..	..	..	1.35	39
26-13	1.20	..	..	..	..	1	3	2	6	1	5	3	3	1	2	..	..	..	2	..	..	..	..	..	..	..	..	..	..	1.35	29
26-14	1.50	..	..	..	1	2	..	3	3	4	5	5	3	7	4	1	2	1	1	2	..	..	..	..	..	..	..	..	1	1.44	45

Total number of F_3 plants..... 911

TABLE 7. BEHAVIOR OF SQUAREHEADEDNESS OF F_2 PLANTS IN F_3. SERIES 13135a, GIANT SQUAREHEAD x MEALY

	Degree of squareheadedness																											Mean	Number of plants
	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85	1.90	1.95	2.00	2.05	2.10		
P_1 Giant Squarehead	..	..	..	..	..	..	..	..	..	..	2	..	1	..	3	1	1	5	4	4	1	4	1	3	2	1	1.77	33
P_1 Mealy	..	..	1	2	6	2	7	4	4	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.14	28
F_1	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	2	1	..	..	..	..	..	..	..	..	..	1.62	5
F_2	1	2	1	2	6	1	7	11	11	11	12	9	11	12	8	5	2	4	..	1	2	1	1	..	..	..	1.36	121
F_3 families																												
Pedigree / Squareheadedness in F_2																												
19-6 1.22	..	..	3	9	12	5	7	1	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.07	39
19-16 1.23	..	1	3	5	6	4	2	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.05	22
20-2 1.26	..	..	..	1	1	2	3	1	2	2	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.22	17
18-2 1.26	..	..	..	..	..	1	1	2	2	2	3	1	2	2	..	2	..	..	..	..	..	..	..	..	..	..	1.35	18
19-5 1.28	..	1	..	1	1	5	10	3	5	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.15	27
20-4 1.31	..	..	1	1	4	3	6	..	4	..	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.17	23
19-17 1.32	..	..	1	3	3	6	8	2	5	3	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.16	33
19-12 1.33	..	..	..	..	2	..	1	1	4	2	8	3	4	3	2	..	..	..	1	..	..	..	..	..	..	..	1.36	31
19-2 1.39	..	1	..	1	7	14	9	1	5	1	1	..	..	1	..	..	..	..	1	1	..	..	..	1	..	..	1.18	44
20-10 1.39	..	..	..	..	1	1	3	7	..	3	2	1	1	1	1	..	..	..	..	..	..	..	..	..	..	..	1.25	21
19-9 1.40	..	..	..	..	1	..	3	3	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.19	9
19-11 1.42	..	..	..	..	1	3	4	3	5	8	6	3	3	..	..	..	..	1	..	1	..	..	..	..	..	..	1.30	38
19-7 1.44	..	..	1	..	..	1	2	2	4	4	3	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.26	20
18-1 1.45	..	..	1	..	..	..	1	6	6	5	5	1	..	1	..	1	..	..	..	..	..	..	..	..	..	..	1.28	27
20-6 1.46	1	1	..	..	..	1	2	4	3	1	1	3	1	..	..	1	..	1	..	..	..	..	..	..	..	..	1.26	20
19-3 1.47	..	..	..	1	1	..	5	4	4	8	6	1	5	5	2	2	..	..	1	..	..	..	..	..	..	..	1.34	45
19-8 1.47	..	..	1	..	5	6	8	5	6	3	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.16	35
20-8 1.47	..	..	..	1	2	..	4	3	3	2	4	..	1	2	..	..	..	..	..	..	..	..	..	..	..	..	1.25	22
19-14 1.48	..	..	1	..	1	5	5	1	4	..	2	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	1.20	21
20-3 1.49	..	..	..	..	1	1	1	4	2	2	1	3	..	..	1	1	..	..	..	..	..	..	..	..	..	..	1.29	17
19-4 1.50	..	..	..	..	..	..	1	3	3	2	2	3	1	3	1	..	1	1	..	..	..	..	..	..	..	..	1.37	21
19-18 1.50	..	..	..	..	..	..	..	..	1	2	8	6	4	4	2	2	..	..	1	..	..	..	..	..	..	..	1.43	30
20-9 1.50	..	1	..	1	4	1	7	7	5	2	1	4	1	1	..	..	..	..	..	..	..	..	..	..	..	..	1.21	35
19-15 1.51	..	..	..	..	..	..	2	6	3	6	4	4	1	2	1	1	..	1	..	..	..	..	..	..	..	..	1.33	31
19-20 1.52	..	..	..	..	..	1	..	2	5	2	7	3	..	2	1	1	1	1	..	..	..	..	..	..	..	..	1.36	26
20-1 1.54	..	..	..	..	1	3	3	6	4	5	2	3	1	1	..	..	..	..	..	..	..	..	..	..	..	..	1.25	29
20-12 1.54	..	1	1	4	5	3	6	7	3	2	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.15	35
20-5 1.55	..	1	..	..	..	..	1	2	2	4	1	3	1	4	..	..	1	..	..	..	..	..	..	..	..	..	1.34	20
18-3 1.55	..	..	1	2	5	3	8	7	7	6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.18	39
20-13 1.56	..	..	2	1	1	4	6	1	4	1	2	4	3	1	1	..	..	..	..	..	..	..	..	..	..	..	1.24	31
19-19 1.57	..	..	1	..	1	2	4	2	3	2	2	1	1	1	..	1	..	..	..	..	..	..	..	..	..	..	1.25	21
20-7 1.59	..	..	..	..	..	1	..	2	5	2	7	3	..	2	1	1	1	1	..	..	..	..	..	..	..	..	1.36	26
19-13 1.64	..	..	..	..	..	2	1	3	6	5	9	2	3	..	2	..	1	..	1	..	..	..	..	1	..	..	1.35	36
19-1 1.72	..	..	..	2	..	3	8	7	7	8	10	6	6	2	..	..	..	1	..	..	..	..	..	..	..	..	1.29	60
20-11 1.74	..	..	1	1	1	2	4	..	2	2	4	1	..	1	1	2	1	2	..	..	..	..	..	..	..	..	1.32	25
19-10 1.88	..	..	..	1	2	6	6	6	3	..	3	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.18	28

Total number of F_3 plants 1,022

That a segregation of forms is taking place is quite evident. The F_3 distributions shown in table 6 are arranged in the order in which they were planted, so that the differences may not be ascribed to environmental conditions. Cultures 24-8, 25-3, and 25-4 show notable differences in distribution and mean from the cultures growing next to them. Similarly, in table 7, where the F_3 distributions are arranged according to the degree of squareheadedness of the F_2 plants, the difference in squareheadedness of cultures 19-17, 19-18, and 19-19, and many others, is to be noted. The progeny of plant 19-17, representing a line in which none of the plants were squareheads, grew immediately next to a row, 19-18, which produced only squareheads, thirty in all.

In order to show that the variations noted in the F_3 are not chance variations but are hereditary, the curves shown in figure 78 were plotted,

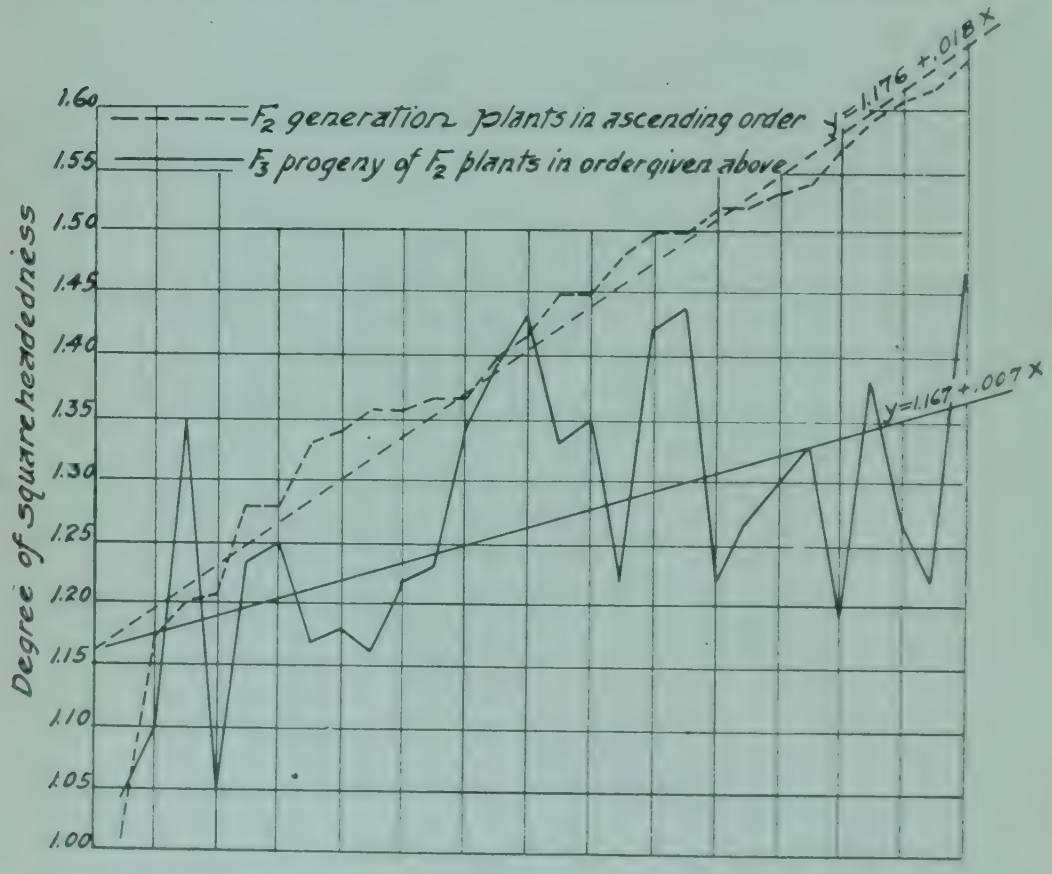

FIG. 78. RELATION OF DEGREE OF SQUAREHEADEDNESS BETWEEN F_2 PARENT PLANTS AND THEIR PROGENY

based on the F_3 data of series 13140a (table 6). Two sets of curves are shown in this figure. The dotted curve represents the degree of squareheadedness of the F_2 plants, and the solid curve represents the means of the F_3 in the order of squareheadedness of the F_2 plants.

The inclination of the straight line fitted to the curve of the F_3 progeny shows that in a general way the degree of squareheadedness of the progeny is determined by the degree of squareheadedness of the F_2 parent plants. A few words of explanation may be given to account for the constant rise and fall of this curve. Since the F_3 figures represent, respectively, the means of approximately thirty individuals, there is no question that they are dependable, and the differences between the means of the F_3 plants show their comparative genotypic differences. Since the mean of the F_3 in material having a mode of inheritance such as this character fluctuates more or less around the degree of squareheadedness of the F_2 form planted, it may be assumed that, had the F_2 plants been grown in the same year as and under conditions similar to those under which the F_3 were grown, the average degree of squareheadedness of the developed heads of the F_2 planted would have approached more nearly the mean of their progeny. Because of the large number of plants that had to be measured, it was not found practicable to measure several heads from each F_2 plant. A developed head was taken at random from each of the envelopes containing the heads of each plant, and was measured. Since different heads in a single plant vary greatly in squareheadedness, the developed head selected at random does not necessarily show the true phenotype. Therefore, the zigzag nature of the F_3 curve should not be ascribed to inconsistent variations, but to inability to ascertain the true degree of squareheadedness of the F_2 by a single measurement, or even more, of the heads of a single plant.

The difference between the slope of the straight line of the F_2 curve and that of the F_3 is due to two conditions. In the first place, while the F_2 curve represents individual plants of a single frequency distribution, the F_3 curve represents the means of such distributions. In the second place, as the mean represents the average of all plants exhibiting variations, slight or extreme in either direction, the means of the F_3 cannot vary as much as the individuals of the F_2 in which the extremes

of the frequency distribution are also included. The slope of the fitted straight line of the F_3 means could therefore not be expected to be as steep as that of the F_2-generation plants.

Squareheadedness is not peculiar to the lax form commonly known as *squarehead*. It may be present or absent in other forms also. The *compactum* forms usually are squareheaded but there are also many which are not. In the examples that follow it is shown that squareheadedness introduced by a club has the same effect on the forms of the succeeding generations as does squareheadedness introduced by the ordinary lax squarehead.

The dense squarehead of the compacto-capitatum form used in this study was that known as *Dale Gloria* (Plate LXVII, upper, 5). This form is very dense and has an average internode length varying usually from 1.2 to 1.7 millimeters. Its degree of squareheadedness ranges from low to high, as shown in table 8. With very dense wheats such as Dale

TABLE 8. INHERITANCE OF SQUAREHEADEDNESS IN A SQUAREHEAD X COMPACTUM CROSS
(Series 13173a, Dale Gloria x New Soules)

	Degree of squareheadedness																				Mean	Number of plants
	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85	1.90		
Dale Gloria	1	1	1	2	1	..	4	1	..	2	..	2	..	..	1	1	..	..	..	..	1.28	17
New Soules	..	..	..	..	..	..	..	..	..	..	..	2	..	3	..	3	2	2	1	2	1.71	15
13173a F_1	..	..	..	..	..	..	..	..	..	..	..	1	..	1	..	..	2	..	..	..	1.65	4
13173a F_2	..	..	..	4	..	1	2	3	5	5	4	3	1	3	2	1	3	2	2	..	1.46	41

Gloria, there is a certain limit beyond which the internodes do not shorten further. This is particularly true when the terminal spikelets are fertile, for development of a spikelet and development of adjacent parts—glumes, nodes, internodes—seem to go hand in hand. A slight increase in the length of the terminal internodes of heads having an internode length in this region as short as 0.8 to 1.2 millimeters, greatly lowers the degree of squareheadedness. This accounts for the presence of forms of a low degree of squareheadedness among Dale Gloria plants.

In a cross between Dale Gloria and New Soules (series 13173a, table 8), in which both parents were squareheaded, the F_2 plants were found to be practically all in the squarehead classes. There were a few in the non-squarehead classes but these were all dense forms like Dale Gloria.

In a cross such as this, there is also an independent segregation of density in the F_2 generation. Half of these F_2 plants were carried through F_3. The F_3 forms were practically all squareheaded. In some cases there were a few non-squareheads but these were in a very low proportion and probably were genotypically squareheads. As far as squareheadedness is concerned, the Dale Gloria x New Soules cross behaved like any squarehead x squarehead cross, such as those shown in table 4 (page 815).

When Dale Gloria is crossed with *vulgare* forms (table 9), the distri-

TABLE 9. INHERITANCE OF SQUAREHEADEDNESS IN VULGARE x COMPACTUM CROSSES

(13214a, Turkey x Dale Gloria; 1337a, Turkish Amber x Dale Gloria; 13172a, Mealy x Dale Gloria)

	Degree of squareheadedness																						Mean	Number of plants
	0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80			
Parent plants																								
Dale Gloria	..	..	..	1	1	1	2	1	..	4	1	..	2	..	2	..	..	1	1	..	..		1.28	17
Turkey	2	3	2	2	1	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..		0.92	13
Turkish Amber	1	..	..	3	6	10	6	4	4	..	..	..	..	..	..	..	..	..	..	..	..		1.04	34
Mealy	..	..	..	1	2	6	2	7	4	4	1	1	..	..	..	..	..	..	..	..	..		1.14	28
F_1 plants																								
13214a	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	1	..	..	..	..			
1337a	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..			
13172a	..	..	..	..	Not recorded				..	..	..	..	..	..	..	..	..	..	..	..	..			
F_2 plants																								
13214a	1	..	5	4	11	10	2	5	9	3	6	3	1	3	2	..	..	..	..	..	..		1.12	65
1337a	..	..	2	1	5	6	7	5	3	9	3	6	4	3	4	2	2	..	1	..	1		1.25	64
13172a	..	1	2	..	2	6	3	3	10	8	6	5	8	5	4	6	4	1	..	2	..		1.31	76

butions of both the F_1 and F_2 generations show a marked resemblance to those produced by squarehead x *vulgare* crosses as shown in table 5 (page 816). The curves of the F_2 in both instances range from the *vulgare* to the squarehead classes. In this case also Dale Gloria behaved as a squarehead; and it is in reality a squarehead, but in addition it happens to carry a density factor.

Two of the crosses in table 9 were carried through F_3. The results were similar to those already observed in tables 6 and 7 (pages 818 and 819). Using class 1.30 as an arbitrary line dividing non-squareheads from squareheads, different F_3 progenies produced non-squareheads and squareheads in different proportions and degrees. There were progenies which consisted of nothing but squareheads, and others which consisted only of non-squareheads.

The question of the inheritance of squareheadedness, and especially that of the relationship of squareheadedness to certain other characters, is considered further in the discussion of inheritance of density. The general facts observed thus far regarding the inheritance of squareheadedness among forms of the *sativum* group may be summarized as follows:

Squareheadedness is not a unit character, but is a resultant of a combination of growth characters which produce shortening of the terminal internodes. The F_2 and subsequent generations show segregation of plants or lines of squareheadedness distinctly varying in degree, but no definite ratios are observed among these. The average degree of squareheadedness of the F_1-generation plants is usually much higher than the mean of the F_2; in some instances in this study it approached that of the squarehead parent. Apparent vigor due to heterosis, and the greater care usually given to F_1 plants, are considered to account for their variation.

Squareheads crossed among themselves or *sativums* crossed among themselves produce, generally speaking, only squareheads or *sativums*, as the case may be, of ranges and means approaching those of the parental forms. The crosses between squareheads and *sativums* show a wide range of variation, but the range and the mean of the F_2 are still determined by those of the parental forms.

Some of the clubs are squareheaded, and these behave as squareheads when crossed with other forms.

RELATION OF THE DEGREE OF SQUAREHEADEDNESS OF THE VULGARE PARENT IN VULGARE X SQUAREHEAD CROSSES, TO THE SQUAREHEADEDNESS OF THEIR PROGENY

The question as to the extent to which the parent plants influence the squareheadedness of their offspring may be determined by examining crosses in which one of the parents is the same in all crosses while for the other parent different forms are used. In table 5 (page 816) a number of series are shown in which different varieties of *vulgare* are crossed with Giant Squarehead. The F_1 and F_2 generations of these crosses are shown graphically in figure 79, in which the crosses are arranged according to the degree of squareheadedness of the *vulgare* parent.

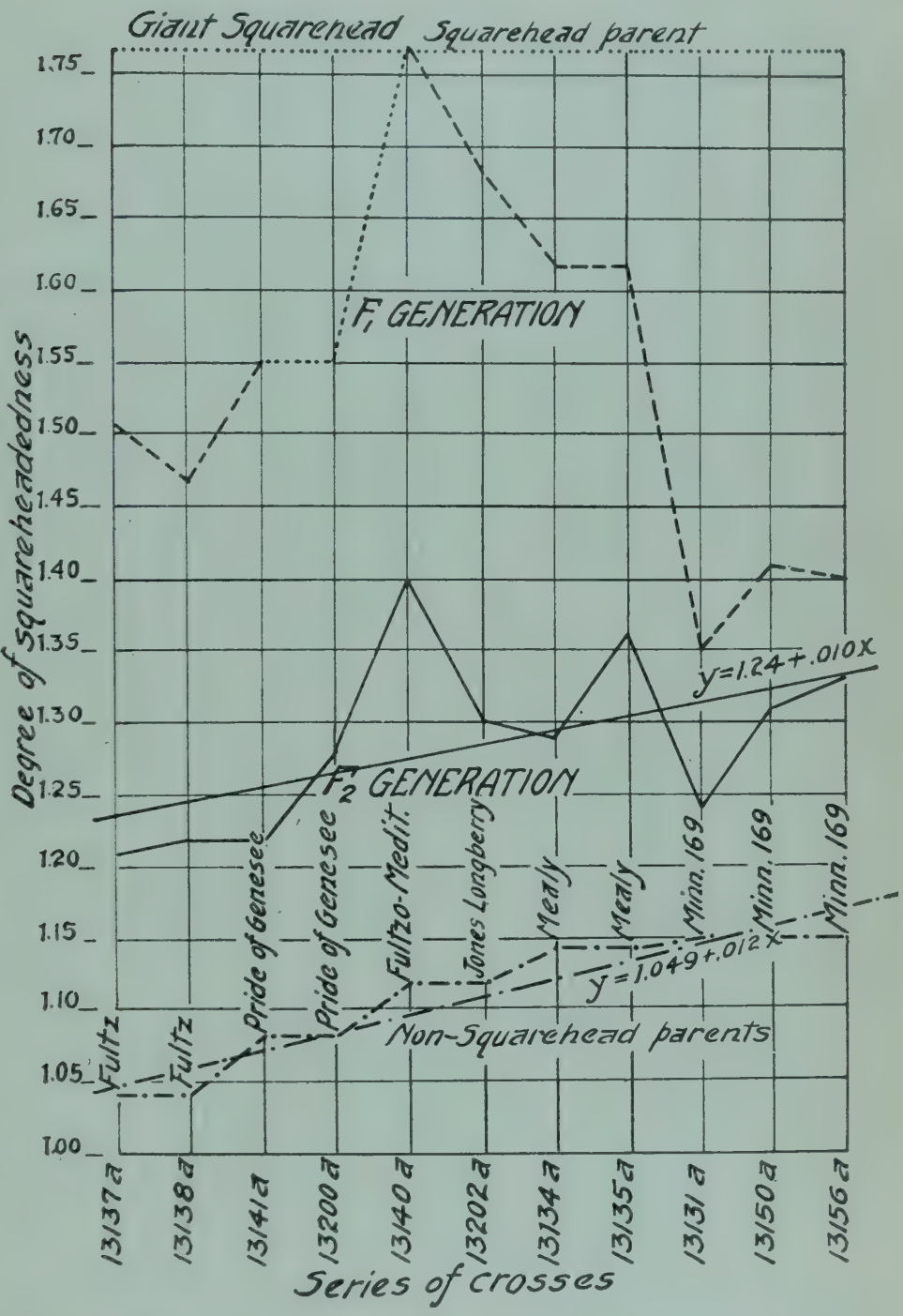

FIG. 79. DEGREE OF SQUAREHEADEDNESS OF PARENTS AND PROGENY WHEN DIFFERENT VULGARE FORMS WERE CROSSED WITH GIANT SQUAREHEAD

The curves representing the means of both the F_1 and F_2 generations show intermediacy between the parental curves. The F_1 curve, as has already been mentioned, shows, as a rule, a higher degree of squareheadedness than the F_2. The F_2 curve shows a general rise of the mean more or less in proportion to that of the *vulgare* parental curve. The F_1 curve, being based on measurements of very few plants, shows great irregularities although it follows the general lines of the F_2 curve.

The curve to be considered is that formed by the F_2 means. Although this curve shows a general rise, it cannot be said that the means of the F_2 increase or decrease directly in proportion with the means of the *vulgare* parents. There are other factors introduced by the *vulgare* parents which, combined with those contributed by the squarehead parent, tend to neutralize or accelerate the production of squareheadedness. For example, Fultzo-Mediterranean produced an F_2 progeny of a very high degree of squareheadedness, and the corresponding rise of the F_1 curve shows that this rise is significant. Mealy and Minnesota 169, although of a higher degree of squareheadedness, produced individuals of lower mean squareheadedness.

The influence of the *vulgare* parent on the squareheadedness of *vulgare* x squarehead-compact crosses is seen in table 9. In the crosses in this table the squarehead-compact parent is Dale Gloria. The *vulgare* parents, Turkey, Turkish Amber, and Mealy, have coefficients of 0.92, 1.04, and 1.14, respectively. The ranking of the F_2 means is in the same order, and coincidently the differences between them are in proportion with the differences existing between the *vulgare* parents.

Because crosses between squareheads produced only squareheads, and those between *vulgare* forms only *vulgare* forms, it cannot be concluded that the degree of squareheadedness of the offspring is entirely dependent on that of the parents, for the determining factor is not the degree of squareheadedness of the parental forms but the peculiar combination of factors introduced by each variety. The mean squareheadedness expressed by a variety is but the resultant of the effects of these factors.

FALSE DOMINANCE OF SQUAREHEADEDNESS

Since the F_2 progeny of a *vulgare* x *vulgare* cross consists only of *vulgare* forms, theoretically one would expect such a cross to produce

only non-squareheads in F_1. This has not always been the case. In table 3 (page 814), giving the results of three Mealy x Jones Longberry crosses, the parental means are 1.14 and 1.12, averaging 1.13, and the means of the F_2-generation plants are 1.12, 1.17, and 1.11, also averaging 1.13. But the F_1-generation plants in all three cases were distinctly squareheads, with means of 1.35, 1.50, and 1.42, respectively. In this paper the figures for squareheadedness or for density of F_1 plants represent the averages of usually from five to ten heads of each plant. If the apparent degree of squareheadedness of the F_1 plants indicated their approximate genotypic make-up, it would be expected that the F_2 distribution would range somewhat near the mean of the F_1 plants. The F_2 plants in these three cases were all *vulgare*, showing that the appearance of F_1 plants of a high degree of squareheadedness in these cases did not show any type of dominance of squareheadedness.

These crosses may be contrasted with the Dawson Golden Chaff x Pride of Genesee cross (13177a), in which the F_1 plants were all *vulgare*, their mean approaching that of the F_2.

The appearance of squareheads in the F_1 generations of series 13158a, 13178a, and 13179a, and the absence of such forms in 13177a, may be accounted for by the supposition that in the first three crosses the combinations of growth factors contributed by the parents were favorable to the production of squareheads, while those contributed by the parents in series 13177a were not favorable.

The presence of squareheads in F_1 and their total absence in F_2 in series 13158a, 13178a, and 13179a, may be regarded as cases of false dominance.

RELATION OF WIDTH OF CULM TO SQUAREHEADEDNESS

The part of the culm below the base of the spike tends to be wider in squareheads than in heads of uniform internode length. The data here considered were taken on the progeny of a lax squarehead x *vulgare* cross, which was not as favorable a material for the study of this character as would have been some other crosses in which a more intense squarehead was used. The results, however, were satisfactory enough to illustrate the degree of correlation between squareheadedness and width of culm.

In taking measurements for squareheadedness of the F_2 generation of series 13135a, the width of the culms of some 260 heads was measured also. The measurement was taken about 2 centimeters below the basal rachis internode. The resulting data are shown in correlation form in table 10. The coefficient of correlation in this distribution is 0.465 ± 0.033, which is significant.

TABLE 10. CORRELATION BETWEEN DIAMETER OF CULM AND SQUAREHEADEDNESS (Series 13135a, Giant Squarehead × Mealy)

Diameter of culm (millimeters)	Degree of squareheadedness									
	0.8	0.9	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7
1.4			1							
1.6			1							
1.8	1	4	9	10	3	1		1		
2.0	1	11	25	28	12	8	1			
2.2		2	15	18	8	5	4	4		
2.4		3	7	12	15	13	5	2	1	
2.6			1	2	6	7	6	2		1
2.8					3	1	2			

$r = 0.465 \pm 0.033$

The writer considers this correlation as not due to any form of linkage but as a direct result of squareheadedness, which is caused in turn by the shortening, or rather hampering of the development, of the terminal part of the spike due to pressure produced by rapid development of the culm internode immediately at the base of the head, and to the failure of the sheath enveloping the spike to grow at a corresponding rate. When the longitudinal growth of the culm internode is checked or retarded, growth naturally takes place in other directions, often causing a thickening of the culm wall. A similar thickening of the wall of the culm occurs also in non-squarehead dense plants and more pronouncedly in squarehead dense plants. In these cases, however, the thickening seems to be due to the presence of the density factor, which shortens the culm internode length as well as the length of the rachis internode. Due to dwarfing, the plant cannot grow in height. The food produced constantly by the plant is stored partly in the culm, thus increasing the thickness of its walls.

The club wheat owes its ability to stand erect in the presence of strong winds to the presence of the density factor, which, as mentioned above, produces thickening of the culm and incidentally of other parts. This factor, which is later considered at length, causes the shortening of the culm also, without affecting the number of nodes. The shortening of the culm internodes increases the number of nodes to each unit of length, thereby giving the culm added strength; moreover, the shortening of the culm lowers the leverage. These three conditions, direct or indirect results of the presence of the density factor, are the chief causes of the non-lodging quality of dense wheat.

INHERITANCE OF SQUAREHEADEDNESS IN SPELT X SATIVUM CROSSES

In crosses wherein the spelt character has been introduced, the curve of the F_2 generation is very distinctly skewed near the extreme of the range on the side of the non-squarehead classes (table 11). True spelts

TABLE 11. SQUAREHEADEDNESS IN SPELT X SATIVUM CROSSES

	Degree of squareheadedness																															Mean	Number of plants
	0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85	1.90	1.95	2.00	2.05	2.10	2.15	2.20				
13125a Crimean x White Spelt	No squareheads																																
13260a White Spelt x Turkey	No squareheads																																
13216a Giant Squarehead x White Spelt	3	12	12	11	14	5	3	2	1	1	3	..	2	3	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.01	73
13255a White Spelt x Dale Gloria	5	7	10	2	11	4	6	4	2	..	7	3	2	1	1	2	2	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	1.10	71
3085a Black Bearded Spelt x Jones Longberry	..	..	..	4	17	4	6	3	2	1	..	1	..	..	1	2	..	..	2	1	..	..	1	..	2	1	1	..	1	..	..	..	1.24	50

differ in their ability to carry the factors producing squareheadedness. It cannot be determined from the appearance of the spelt plants whether or not they carry the squareheading factors, as the spelt character acts as an inhibitor for squareheadedness. In fact, the presence of a large number of individuals in the non-squarehead classes of spelt x *sativum* crosses is the result of the presence of a large number of spelts, which, although carrying the squareheadedness factors, were themselves non-

squareheads because they carried also the spelt factor, which, as stated above, acts as an inhibitor for the squarehead character.

Five crosses between spelts and *sativums* are shown in table 11.[5] Series 13125a and 13260a, which were crosses between *vulgare* and White Spelt, produced F_2 generations composed of non-squareheads only. When this same spelt form was crossed with Giant Squarehead (series 13216a), a number of squareheads were produced in F_2. The White Spelt x Dale Gloria cross (13255a) also showed a fair number of squareheads (Plate LXVII, upper, 6 to 12).

From these results it is seen that the White Spelt does not carry the necessary factors for squareheadedness, since when it was crossed with *vulgare* it produced no squareheads. Squareheads appeared only when a squarehead form was used as the *sativum* parent.

These four crosses were carried through F_3. The first two crosses produced practically no squareheads; a few were obtained, but they were not tested to ascertain their stability. The remaining crosses produced F_3 progeny which were composed of forms of various degrees of squareheadedness. Since the spelt factor acted as an inhibitor, the spelts of the F_3 showed no squareheadedness. The non-spelts produced curves similar to those shown in tables 6 and 7.

That there was no so-called repulsion between the spelt and squareheadedness factors was evident from the reappearance of squareheads among the progeny of some F_2 spelts, and from the absence of squareheads among the offspring of other F_2 spelts.

Another spelt form, known as Black Bearded Spelt, when crossed with a *vulgare*, Jones Longberry (series 3085a), produced a large number of squareheads. These forms were more intensely squareheaded than those produced by the White Spelt x Giant Squarehead cross (13216a).

About ten spelt x *vulgare* crosses, with Black Bearded Spelt as one of the parents, were examined by the writer, and in every case there were a large number of squareheads in the progeny, most of which were semi-dense.

The progeny of cross 3085a were not carried through F_2, but another

[5] The F2 segregations of these crosses were in the proportion of 3 spelts or spelt-like forms to 1 *sativum*.

cross between this same Black Bearded Spelt and a *vulgare* showed that most of the squareheads bred true.

If it is recalled that some of the F_2 spelts of the squarehead x White Spelt cross produced squareheads in F_3 while others that were phenotypically like the former did not, it will not be difficult to understand how the Black Bearded Spelt could have produced different results from those of the White Spelt. It appears, from these examples, that spelts may carry the squareheadedness factors the same as do squarehead *sativums* themselves, but due to the presence of the spelt factor, which acts as an inhibitor, such spelts do not appear squareheaded.

This leads to the consideration of another condition. Since the presence of squareheadedness cannot be detected without a genetic analysis, one may come across a spelt form which, crossed with *vulgare,* may sometimes yield squareheads and sometimes not. Either such a spelt is heterozygous with respect to squareheadedness, or the variety to which it belongs has not been stabilized with respect to this character. As the investigator is guided by apparent characters in purifying a line or in calling it a pure line, he cannot detect the segregation of non-detectable factors which is going on within his selected line.

EFFECT OF THE SPELT FACTOR ON SQUAREHEADEDNESS

In the discussion of the inheritance of squareheadedness in spelt x *sativum* crosses, it was mentioned that the spelt factor inhibited square-

TABLE 12. RELATION OF SQUAREHEADEDNESS TO SPELTING
(Series 13216a, Giant Squarehead x White Spelt)

Degree of spelting	Degree of squareheadedness															
	0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55
1	1	3	3	3	2											
2	1	2	1	1		2										
3	1		1	1	2	2										
4		1	3	1	1											
5		2	2	1	3		1									
6		1	1	3	2											
7		1			1			1								
8		2		1	2					1						
9			1		1	1	2	1	1		1		2	1		1
10											2			2		

TABLE 13. RELATION OF SQUAREHEADEDNESS TO SPELTING

(Series 13255a, White Spelt x Dale Gloria)

Degree of spelting	Degree of squareheadedness																				
	0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75
1	3	3	6	2		1			1											
2	2	1	3		2		2													
3		1	1		3		2	1			1									
4					1	1	2													
5		2			1	1		1												
6												1								
7					1			1			2									
8																				
9															1	1				
10					3	1		1	1		4	2	2	1		1	2	1		1

TABLE 14. RELATION OF SQUAREHEADEDNESS TO SPELTING

(Series 3085a, Black Bearded Spelt x Jones Longberry)

Degree of spelting	Degree of squareheadedness																					
	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85	1.90	1.95	2.00	2.00 +
1	2	5	1		1																		
2	1	2	2	2	1																		
3		4																					
4		1			1																		
5		2		2																			
6																							
7		3		1																			
8						2																	
9							1		1													1	
10	1		1	1								1	2			2	1			1		1	3

headedness. The object here is to show to what extent this inhibition takes place. To illustrate this, three types of crosses are used. The first is the Giant Squarehead x White Spelt cross (table 12); the second is White Spelt x Dale Gloria (table 13); and the third is Black Bearded Spelt x Jones Longberry (table 14). In the first two crosses, squareheadedness is introduced by a lax squarehead and a dense squarehead, respectively, and in the last cross it is introduced by the spelt.

The F_2 plants in these tables are classified into ten arbitrary classes of spelting. The spelts in such crosses exhibit the spelt character in various degrees. Those showing it in an intense form are placed in class 1; classes 2, 3, 4, and so on up to 9, show various degrees of dilution of the character; the plants in class 10 are all *sativum* forms, and lack the spelt altogether.[6]

The distribution of the plants with respect to spelting and squareheadedness, as shown in tables 12 to 14, seems to depend to a great extent on the types used as parents. Different spelts crossed with different *sativums* show different modifications. All crosses, however, show the following general distribution: Spelts of classes 1 to 5 inclusive arrange themselves more or less within the non-squarehead classes 0.80 to 1.15. There is a slight tendency in spelt classes 3 to 5 to move the mean toward 1.15. As the classes approach the *sativum* type, the shifting of the mean toward the more squareheaded classes is accelerated in geometrical proportion.

The spelt factor, then, does not prevent squareheadedness altogether, but plants that are heterozygous spelts or those that carry modifiers tending to dilute this spelt character are very much more likely to be squareheaded than plants that are intensely spelted. Squareheadedness in spelts, however, is always of a low degree.

INHERITANCE OF SQUAREHEADEDNESS IN SPECIFIC CROSSES

It has already been shown (page 829) that when Black Bearded Spelt is crossed with a *sativum* of a uniform rachis internode length, an appreciable number of squareheaded forms appear in the F_2. Squareheads may be obtained also when a *vulgare* is crossed with other species. In table 15 the progeny of a number of interspecific crosses are classified into two groups, the first containing forms resembling the *sativum* type and the second including all the other forms. Their degree of squareheadedness is represented in the usual manner.

In all series a large proportion of the *sativum* or *sativum*-like forms were squareheads. The segregates belonging to other species were practically all non-squareheads.

[6] The genetics of the spelt character with reference to the crosses under consideration has been fully discussed in a recent paper (Leighty and Boshnakian, 1921).

TABLE 15. DEGREE OF SQUAREHEADEDNESS IN SPECIES CROSSES. F_2 DATA

3032 Salt Lake Club x Kahle (*Triticum durum*)
3034 Gharnovka (*T. durum*) x Black Bearded Spelt (*T. spelta*)
1312a Poole (*T. vulgare*) x Alaska (*T. turgidum*)
1328a Satisfaction (*T. vulgare*) x Alaska (*T. turgidum*)
1360a Jones Paris Prize (*T. vulgare*) x Kubanka (*T. durum*)

F_2 generation results	Degree of squareheadedness																									Mean	Number of plants
	0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85	1.90	1.95	2.00†		
3032—																											
Sativum and *sativum*-like forms	..	..	..	4	..	2	2	..	2	1	4	6	5	1	2	2	..	2	..	2	..	..	..	..	..	1.32	35
All other forms	..	..	1	3	2	1	1	2	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.04	11
3034—																											
Sativum-like forms *	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	1	..	..	1	..	..	..	2	1 81	5
All other forms	..	..	2	7	24	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	0.99	36
1312a—																											
Sativum and *sativum*-like forms	..	..	..	2	1	2	..	2	4	2	1	..	2	..	1	..	..	..	1	..	..	2	..	..	2	1.38	22
All other forms	..	4	13	8	13	8	4	1	2	2	1	..	1	..	..	..	..	..	..	..	..	..	..	..	1	1 08	58
1328a—																											
Sativum and *sativum*-like forms	..	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	1	1	..	..	..	..	..	..	4	1.69	8
All other forms	3	3	5	4	7	5	1	5	2	1	2	1	..	..	1	..	..	..	1	..	..	..	..	..	..	1.10	41
1360a—																											
Sativum and *sativum*-like forms	..	..	..	..	..	1	1	..	..	3	..	..	..	2	1	..	..	1	..	..	..	..	..	..	..	1.33	9
All other forms	..	..	1	..	2	5	1	..	3	..	..	1	..	..	..	..	..	2	..	..	..	..	..	..	..	0.15	15

*Series 3034 did not produce true *sativums* in the F_2.
†2.00 or over.

Squareheadedness is not confined, however, to the *sativum* form. Other species, with the exception of the wild wheat, may show this character, particularly the segregates of the *durum*, the *turgidum*, and the *polonicum* types and even the *dicoccum* type. But squareheadedness in these forms is of low degree and is comparatively rare (Plate LXVII, lower).

The analysis of the F_2 forms in specific crosses presents a difficult task because a large number of specific forms appear, of which some are developed and others are very mediocre or sterile with different tendencies toward squareheadedness.

SUMMARY

Squareheadedness, being the result of a combination of growth characters, shows a complex mode of inheritance. Simple mendelian segregations were not obtained in these experiments.

In the F_3 generation there were obtained plants of different degrees of squareheadedness, ranging from forms which were distinctly compacted at the tip to forms which were denser near the base of the ear.

As a rule the range of variation in F_2 depended on the differences between the extremes of the parental ranges. The means of the F_2 approached the parental means.

The F_1 generation usually had a higher coefficient than the parental mean. Some F_1 progeny of two non-squarehead parents were even distinctly squareheads, but in F_2 none of these forms were obtained. These variations from normal expectations are ascribed to heterosis and to greater feeding area.

A coefficient of correlation of 0.465 ± 0.033 was found between width of culms and squareheadedness.

The purely spelt forms were found not to be affected by the factors producing squareheadedness. The more the spelts approached the *sativum* type, the more they were found to be affected. Speltoid forms did carry these factors, as is shown by the fact that among their *sativum* progeny a large number of squareheads of varying intensities were found.

Certain spelts when crossed with a *vulgare* form will produce a large number of squareheads in F_2. Others will produce only non-squareheaded *sativum* forms.

Squarehead forms may be produced by crossing *Triticum vulgare* with other wheat species.

THE GENETICS OF DENSITY

The discussion in the following pages deals with the genetics of compactness of the dense forms of wheat, and especially of *Triticum compactum*, the club wheat. The name *club wheat* seems to have been originally given to the squareheads, but at present it is applied almost exclusively to the *compactum* form.

The index of compactness used in this paper is the average rachis internode length. The index is found by dividing the length of the rachis in millimeters by the number of rachis internodes. The denser or more compact the head, the shorter is the length of the rachis internode.

Although there are numerous grades of compactness, the rachis internode length of what is usually called a club wheat does not exceed 2.25 millimeters. The mean density of the club used in the studies presented in this paper was about 1.4 millimeters.

INHERITANCE OF DENSITY IN CROSSES BETWEEN TRITICUM COMPACTUM AND OTHER FORMS OF THE SATIVUM GROUP

The studies of density herein discussed were made on crosses between Dale Gloria (Plate LXVII, upper, 5) and a number of lax forms consisting of both squarehead and *vulgare* types. The mean density of the Dale Gloria parent was 1.41 millimeters; the means of the lax parents were in the neighborhood of 4.50 millimeters.

The F_1 hybrids were all dense, but not quite as dense as Dale Gloria (table 16). They varied from 1.80 to 2.40, depending on the cross.

TABLE 16. SEGREGATION OF DENSITY IN CROSSES BETWEEN DALE GLORIA (COMPACTUM) AND LAX FORMS

13174a Extra Early Windsor x Dale Gloria
13173a New Soules x Dale Gloria
13172a Mealy x Dale Gloria
13214a Turkey x Dale Gloria
13215a Seneca Chief x Dale Gloria
1337a Turkish Amber x Dale Gloria
13213a Red Wave x Dale Gloria

	Degree of squareheadedness																							Mean	Number of plants
	1.3	1.5	1.7	1.9	2.1	2.3	2.5	2.7	2.9	3.1	3.3	3.5	3 7	3.9	4.1	4.3	4 5	4.7	4.9	5 1	5 3	5 5			
Parent plants																									
Dale Gloria	6	9	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..		1.41*	18
Extra Early Windsor	..	..	..	..	..	..	..	..	..	..	..	..	..	3	9	5	4	3	..	..	..	..		4.25	24
New Soules	..	..	..	..	..	..	..	..	..	1	..	4	8	5	7	4	1	..	..	..	..	..		3.89	30
Mealy	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	3	3	7	..	..	..	..		4.53	14
Turkey	..	..	..	..	..	..	..	..	..	..	..	..	..	2	3	4	3	2	1	..	..	..		4.34	15
Seneca Chief	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	3	3	4	..	..	..	..		4.48	11
Turkish Amber	..	..	..	..	..	..	..	..	..	..	..	1	..	..	3	2	4	3	8	7	3	3		4.82	34
Red Wave	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	3	2	5	1	1		4.94	14
F_1 plants																									
13174a	..	..	2	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..		1.80	4
13173a	..	..	..	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..		1.90	4
13172a	Not recorded																								
13214a	..	..	..	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..		2.10	2
13215a	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..		1.90	1
1337a	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..		2.30	1
13213a	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..		2.40	2
F_2 plants																									
13174a	1	6	10	7	11	5	..	..	..	..	1	5	3	2	5	2	1	1	1	..	..	..		2.59	61
13173a	4	7	13	8	6	..	1	..	..	..	1	3	1	2	1	1	..	..	..	..	..	..		2.33	48
13172a	..	5	7	7	16	7	9	3	1	..	2	1	4	4	2	2	2	4	..	..	..	..		2.64	76
13214a	..	1	9	5	7	7	12	6	4	3	..	..	..	..	3	2	4	1	2	..	1	..		2.74	67
13215a	1	7	5	8	26	5	1	1	..	..	..	1	5	..	1	2	2	1	..	1	..	..		2.49	67
1337a	..	1	1	9	7	8	6	2	6	3	..	..	1	3	4	4	5	2	1	..	..	2		3.04	65
13213a	..	2	2	5	8	11	8	4	4	3	..	..	..	..	2	3	2	2	2	1	..	2		2.87	61

*This figure represents the arithmetical average, not the mean of the frequency distribution.

The density curves of the F_2-generation plants, unlike those of the squarehead x non-squarehead crosses, were all discontinuous, consisting of two well-defined curves. In each case the curve of the dense classes contained about three times as many individuals as that of the lax classes. The proportions of these forms are given in table 17. In five cases the

TABLE 17. PROPORTIONS OF DENSE AND LAX SEGREGATES OF THE F_2 GENERATIONS OF CROSSES BETWEEN DALE GLORIA (COMPACTUM) AND OTHER LAX FORMS

Series	Dense forms		Lax forms		Deviation	Probable error	Dev. / P. E.	Mean of dense plants	Mean of lax plants	Mean of all plants	Total number of individuals
	Number obtained	Number expected	Number obtained	Number expected							
13174a	40	45.7	21	15.2	−+5.8	±2.28	2.54	1.88	3.95	2.59	61
13173a	39	36.0	9	12.0	+−3.0	±2.02	1.48	1.74	3.74	2.33	48
13172a	55	57.0	21	19.0	−+2.0	±2.55	0.78	2.11	4.04	2.64	76
13214a	54	50.2	13	16.7	+−3.7	±2.39	1.55	2.30	4.51	2.74	67
13215a	54	50.2	13	16.7	+−3.7	±2.39	1.55	1.98	4.12	2.40	67
1337a	43	48.7	22	16.2	−+5.8	±2.36	2.46	2.34	4.40	3.04	65
13213a	47	45.7	14	15.2	+−1.2	±2.28	0.53	2.33	4.67	2.87	61
Total	332	333.7	113	111.2	−+1.8	±6.16	0.29	2.09	4.20	2.66	445

deviations from the calculated ratios exceeded somewhat their probable errors, and in two cases the deviations were well within the probable errors. Summing up the results of these seven crosses, of 445 plants obtained in the F_2 generation 332 were dense and 113 were lax; the deviation from the calculated proportions on the 3:1 basis was — + 1.8, which is about one-third of its probable error. These results show that so far as these crosses are concerned the F_2 plants segregate into dense and lax forms in 3:1 ratio, the density being dominant.

Four of these crosses, of which two were with squareheads and the other two with *vulgare*, were carried through the F_3 generation in order to test whether the assumption of the presence of one factor was correct. The results obtained are condensed and given in table 18. Of the 125 F_2 plants tested, 30 were homozygous dense, 67 produced both dense and lax forms, and 28 were homozygous lax. These figures, compared with the calculated proportions—31.2 ± 3.3, 62.5 ± 3.9, and 31.2 ± 3.3, respectively—show a very close agreement with the 1:2:1 ratio. The proportion of plants obtained in each cross taken separately agrees also with the theoretical expectancy, the largest departure being but 25 per cent more than its probable error.

TABLE 18. PROPORTIONS OF HOMOZYGOUS DENSE, HETEROZYGOUS DENSE, AND HOMOZYGOUS LAX PLANTS OF THE F_2 GENERATION OF SERIES TESTED IN THE F_3 GENERATION

	Homozygous dense forms					Heterozygous dense forms					Homozygous lax forms					Total number of plants tested
	Number obtained	Number expected	Deviation	Probable error	Dev. P. E.	Number obtained	Number expected	Deviation	Probable error	Dev. P. E.	Number obtained	Number expected	Deviation	Probable error	Dev. P. E.	
13172a—Mealy x Dale Gloria	9	9.2	−0.2	±1.8	0.11	21	18.5	+2.5	±2.0	1.25	7	9.2	−2.2	±1.8	1.22	37
13173a—New Soules x Dale Gloria	6	7.5	−1.5	±1.5	1.00	16	15.0	+1.0	±1.8	0.55	8	7.5	+0.5	±1.5	0.33	30
13174a—Extra Early Windsor x Dale Gloria	6	6.5	−0.5	±1.5	0.33	13	13.0	0	±1.7	....	7	6.5	+0.5	±1.5	0.33	26
13214a—Turkey x Dale Gloria	9	8.0	+1.0	±1.6	0.63	17	16.0	+1.0	±1.9	0.53	6	8.0	−2.0	±1.6	1.25	32
Total	30	31 2	+1 2	±3 3	0 36	67	62 5	+4 5	±3 9	1 15	28	31 2	−3 2	±3 3	0 97	125

The behavior of each individual F_2 plant of the four crosses under consideration is shown respectively in tables 19, 20, 21, and 22. Of the

TABLE 19. BEHAVIOR OF F_2 PLANTS IN F_3. SERIES 13172a, MEALY (VULGARE) x DALE GLORIA

F_2 pedigree	F_2 density	Mean density of dense F_3 plants	Mean density of lax F_3 plants	Dense plants		Lax plants		Total F_3 plants	Deviation	Probable error	Dev. / P. E.
				Number obtained	Number calculated	Number obtained	Number calculated				
30-11	1.50	1.35	....	29	....	..	....	29	....	....	...
30-21	1.53	1.66	....	22	....	..	....	22	....	....	...
29-9	1.57	1.18	....	6	....	..	....	6	....	....	....
29-8	1.65	1.46	....	20	....	..	....	20	....	....	....
30-2	1.71	1.37	....	22	....	..	....	22	....	....	....
30-14	1.73	1.52	....	24	....	..	....	24	....	....	....
30-5	1.76	1.54	....	24	....	..	....	24	....	....	....
30-18	1.81	1.43	....	28	....	..	....	28	....	....	....
29-4	1.89	1.71	....	18	....	..	....	18	....	....	....
30-7	1.84	1.47	3.08	24	22.5	6	7.5	30	+− 1.5	±1.63	0.92
30-6	1.85	1.72	3.41	33	32.2	10	10.7	43	+− 0.7	±1.92	0.36
30-9	1.90	1.52	3.01	34	33.7	11	11.2	45	+− 0.2	±1.96	1.00
30-8	1.95	1.69	3.56	31	30.7	10	10.2	41	+− 0.2	±1.87	0.11
29-6	2.00	1.44	3.06	18	18.7	7	6.2	25	−+ 0.8	±1.46	0.55
30-19	2.00	1.65	3.00	23	21.0	5	7.0	28	+− 2.0	±1.55	1.29
29-10	2.06	1.80	3.70	25	24.7	8	8.2	33	+− 0.2	±1.68	0.12
30-3	2.10	1.67	3.53	28	27.0	8	9.0	36	+− 1.0	±1.78	0.56
29-3	2.11	2.08	3.30	19	15.7	2	5.2	21	+− 3.2	±1.34	2.39
30-13	2.14	1.70	3.33	34	36.0	14	12.0	48	−+ 2.0	±2.02	0.99
29-12	2.19	2.04	4.03	22	18.7	3	6.2	25	+− 3.2	±1.46	2.19
30-20	2.25	1.83	3.64	22	24.7	11	8.2	33	−+ 2.8	±1.68	1.67
29-1	2.39	1.90	3.15	18	16.5	4	5.5	22	+− 1.5	±1.37	1.09
29-11	2.42	1.72	3.69	30	29.2	9	9.7	39	+− 0.7	±1.82	0.38
30-10	2.43	1.93	3.52	32	27.7	5	9.2	37	+− 4.2	±1.78	2.36
30-1	2.50	2.22	4.23	37	35.2	10	11.7	47	+− 1.7	±2.00	0.85
30-15	2.52	1.85	3.47	28	25.5	6	8.5	34	+− 2.5	±1.70	1.47
29-2	2.53	2.00	3.64	19	19.5	7	6.5	26	−+ 0.5	±1.49	0.33
30-4	2.58	1.81	3.56	27	28.5	11	9.5	38	−+ 1.5	±1.80	0.83
29-14	2.84	1.78	4.26	13	13.5	5	4.5	18	−+ 0.5	±1.24	0.40
Total heterozygous plants				517	501.7	152	167.2	669	+−15.2	±7.55	2.01
30-16	3.28	....	3.39	..	....	16	....	16	....	....	....
30-12	3.55	....	3.36	..	....	23	....	23	....	....	....
30-22	3.75	....	3.12	..	....	20	....	20	....	....	....
30-17	3.84	....	3.43	..	....	17	....	17	....	....	....
29-13	4.16	....	3.88	..	....	20	....	20	....	....	....
29-5	4.27	....	3.65	..	....	17	....	17	....	....	....
29-7	4.44	....	4.08	..	....	5	....	5	....	....	....
Total F_3 plants....								980			

669 heterozygous plants obtained in series 13172a (table 19), 517 were dense and 152 were lax, the deviation from the calculated ratio being about twice its probable error. In series 13173a (table 20), the ratio between the probable error and the deviation from expectation is 1 : 5.22, which is rather high. In series 13174a (table 21) this ratio is 1 : 5.02, and in series 13214a (table 22) it is only 1 : 0.46. All these results, in spite of the differences between observed and calculated ratios which

TABLE 20. BEHAVIOR OF F_2 PLANTS IN F_3. SERIES 13174a, NEW SOUTH (CAPITATUM) x DALE GLORIA

F_2 pedigree	F_2 density	Dense plants		Lax plants		Total F_3 plants	Deviation	Probable error	Dev. / P. E.
		Number obtained	Number calculated	Number obtained	Number calculated				
32-7	1.31	37	....	..	....	37	....	....	
31-11	1.52	23	....	..	....	23	....	....	
32-6	1.52	60	....	..	....	60	....	....	
31-3	1.55	40	....	..	....	40	....	....	
31-9	1.55	35	....	..	....	35	....	....	
32-8	1.62	41	....	..	....	41	....	....	
31-8	1.64	24	27.8	13	9.2	37	−+ 3.8	±1.78	2.13
32-13	1.65	52	58.5	26	19.5	78	−+ 6.5	±2.58	2.52
32-14	1.68	51	54.0	21	18.0	72	−+ 3.0	±2.48	1.21
31-7	1.71	29	31.5	13	10.5	42	−+ 2.5	±1.89	1.32
32-15	1.71	93	99.8	40	33.2	133	−+ 6.8	±3.37	2.02
32-9	1.78	67	67.5	23	22.5	90	−+ 0.5	±2.77	0.18
32-16	1.81	59	63.0	25	21.0	84	−+ 4.0	±2.68	1.49
31-12	1.88	35	32.3	8	10.7	43	+− 2.7	±1.92	1.41
32-5	1.91	46	46.5	16	15.5	62	−+ 0.5	±2.30	0.22
32-10	1.95	62	63.0	22	21.0	84	−+ 1.0	±2.68	0.37
31-1	1.95	30	43.5	28	14.5	58	−+13.5	±2.22	6.08
32-2	2.00	42	39.0	10	13.0	52	+− 3.0	±2.11	1.42
31-2	2.06	40	39.8	13	13.2	53	+− 0.2	±2.13	0.09
31-4	2.09	30	33.0	14	11.0	44	−+ 3.0	±1.94	1.55
32-12	2.15	83	87.8	34	29.2	117	−+ 4.8	±3.16	1.52
32-17	....	62	69.8	31	23.2	93	−+ 7.8	±2.82	2.76
Total heterozygous plants		805	856.5	337	285.5	1,142	−+51.5	±9.87	5.22
31-10	3.40	..	....	37	....	37	....	....	
31-6	3.43	..	....	21	....	21	....	....	
32-4	3.45	..	....	56	....	56	....	....	
32-3	3.80	..	....	69	....	69	....	....	
32-1	3.87	..	....	31	....	31	....	....	
31-5	3.95	..	....	33	....	33	....	....	
31-13	4.19	..	....	24	....	24	....	....	
32-11	4.28	..	....	71	....	71	....	....	
Total F_3 plants						1,720			

they exhibit occasionally, show that so far as these crosses are concerned only one factor is involved in the production of density.

Referring to tables 19, 20, 21, and 22, it will be noticed that while in series 13172a and 13214a the proportion of dense and lax forms agreed rather closely, in series 13173a and 13174a an excess of lax forms was recorded in practically every case. In series 13173a, out of 16 heterozygous plants tested all but three yielded an excess of lax forms, while in series 13174a all but one plant yielded an excess of lax forms.

When wheat plants are grown closely together, the roots occasionally tend to intertwine, and unless the heads show variations of segregating gross characters it is not usually possible to determine whether there are two plants or only one. In crosses between dense and lax plants, in which the segregation is 3:1, out of 16 possibilities there are 9 chances

TABLE 21. BEHAVIOR OF F_2 PLANTS IN F_3. SERIES 13174a
EXTRA EARLY WINDSOR (CAPITATUM) x DALE GLORIA

F_2 pedigree	F_2 density	Mean density of dense F_3 plants	Mean density of lax F_3 plants	Dense plants		Lax plants		Total F_3 plants	Deviation	Probable error	Dev. P. E.
				Number obtained	Number calculated	Number obtained	Number calculated				
34-3	1.31	1.29	....	29	....	..	....	29	....	....	....
34-8	1.40	1.28	....	25	....	..	....	25	....	....	....
34-11	1.55	1.36	....	22	....	..	....	22	....	....	....
33-5	1.55	1.28	....	46	....	..	....	46	....	....	....
33-15	1.85	1.30	....	46	....	..	....	46	....	....	....
33-9	2.00	1.28	....	39	....	..	....	39	....	....	....
33-4	1.70	1.37	3.09	59	64.5	27	21.5	86	−+ 5.5	±2.70	2.04
33-2	1.74	1.57	3.77	56	63.7	29	21.2	85	−+ 7.8	±2.69	2.90
34-4	1.86	1.57	3.69	31	32.2	12	10.7	43	−+ 1.3	±1.92	0.68
34-6	1.95	1.54	3.31	23	24.0	9	8.0	32	−+ 1.0	±1.65	0.61
34-12	1.95	1.69	3.33	23	24.0	9	8.0	32	−+ 1.0	±1.65	0.61
34-5	2.00	1.39	3.32	18	17.2	5	5.7	23	+− 0.7	±1.40	0.50
33-6	2.00	1.54	3.59	49	51.7	20	17.2	69	−+ 2.8	±2.43	1.15
33-7	2.00	1.60	3.34	45	48.0	19	16.0	64	−+ 3.0	±2.32	1.29
33-3	2.00	1.60	3.42	45	50.2	22	16.7	67	−+ 5.3	±2.39	2.22
33-13	2.05	1.60	3.80	47	48.7	18	16.2	65	−+ 1.8	±2.36	0.76
34-10	2.11	1.69	3.48	23	24.0	9	8.0	32	−+ 1.0	±1.65	0.61
33-17	2.20	1.57	3.53	48	52.5	22	17.5	70	−+ 4.5	±2.44	1.84
33-11	2.21	1.65	3.50	51	57.0	25	19.0	76	−+ 6.0	±2.55	2.35
Total heterozygous plants.....				518	558.0	226	186.0	744	−+40.0	±7.96	5.02
33-10	3.30	....	3.20	..	....	22	....	22	....	....	....
34-1	3.50	....	3.35	..	....	34	....	34	....	....	....
33-1	3.71	....	3.35	..	....	35	....	35	....	....	....
34-9	3.95	....	3.86	..	....	18	....	18	....	....	....
34-7	3.96	....	3.62	..	....	24	....	24	....	....	....
33-16	4.05	....	3.33	..	....	42	....	42	....	....	....
33-12	4.42	....	3.77	..	....	51	....	51	....	....	....
Total F_3 plants.....								1,177			

that a dense plant will grow next to a dense plant, 6 chances that it will grow next to a lax plant (or that a lax plant will grow next to a dense plant), and 1 chance that a lax plant will grow next to a lax plant. In other words, where entangling exists due to close planting, there will be six cases in which this condition will be detected and lax and dense plants separated, and nine cases in which it will be overlooked because the heads will all be dense and will show no visible difference. If this factor of entanglement is present whereby some dense plants are overlooked, theoretically there will be fewer dense plants than are expected.

If the degree of experimental error introduced by this factor is calculated, it will be found that if, among 50 plants forming a segregating population, there are two or three cases in which a dense plant has been interlaced with its neighbor and is not separated, the differences between recorded and theoretical ratios will be about as great as those shown in tables 20 and 21.

TABLE 22. BEHAVIOR OF F_2 PLANTS IN F_3. SERIES 13214a, TURKEY (VULGARE) x DALE GLORIA

F_2 pedigree	F_2 density	Mean density of dense F_3 plants	Mean density of lax F_3 plants	Dense plants		Lax plants		Total F_3 plants	Deviation	Probable error	Dev. / P.E.
				Number obtained	Number calculated	Number obtained	Number calculated				
38-8	1.72	1.46	....	68	....	..	....	68	....	....	....
39-9	1.91	1.76	....	45	....	..	....	45	....	....	
38-12	1.95	1.41	....	97	....	..	....	97	....	....	
38-14	1.95	1.49	....	85	....	..	....	85	....	....	
39-4	2.06	1.66	....	33	....	..	....	33	....	....	
38-11	2.16	1.51	....	59	....	..	....	59	....	....	
38-9	2.33	1.61	....	83	....	..	....	83	....	....	
38-13	2.39	1.58	....	57	....	..	....	57	....	....	
38-4	2.75	1.49	....	44	....	..	....	44	....	....	
40-3	1.57	1.37	3.18	73	57.8	4	19.2	77	+−15.2	±2.56	5.94
40-6	2.11	1.65	3.23	47	41.3	8	13.7	55	+− 5.7	±2.17	2.63
38-15	2.11	1.58	3.20	35	40.5	19	13.5	54	−+ 5.5	±2.15	2.56
40-1	2.28	1.64	3.15	42	48.0	22	16.0	64	−+ 6.0	±2.34	2.56
39-3	2.35	1.67	3.28	29	31.5	13	10.5	42	−+ 2.5	±1.89	1.32
40-2	2.35	1.91	3.51	53	54.8	20	18.2	73	−+ 1.8	±2.50	0.72
39-2	2.53	1.76	3.44	52	51.7	17	17.2	69	−+ 0.2	±2.39	0.08
38-2	2.53	2.08	4.30	10	12.8	7	4.2	17	−+ 2.8	±1.20	2.33
40-7	2.57	1.92	3.77	46	42.0	10	14.0	56	+− 4.0	±2.19	1.83
38-10	2.61	1.96	3.51	30	30.0	10	10.0	40	0.0	±1.85	
39-5	2.75	1.87	3.32	24	23.3	7	7.7	31	+− 0.7	±1.63	0.43
40-8	2.79	2.13	3.78	48	58.5	30	19.5	78	−+10.5	±2.58	4.07
38-5	2.89	2.16	4.09	23	24.0	9	8.0	32	−+ 1.0	±1.65	0.61
38-7	2.90	2.23	3.72	47	45.0	13	15.0	60	+− 2.0	±2.26	0.88
40-4	2.94	2.18	3.59	48	45.8	13	15.2	61	+− 2.2	±2.28	0.96
40-10	3.00	2.20	3.83	51	48.8	14	16.2	65	+− 2.2	±2.36	0.93
39-6	3.06	2.28	3.89	73	71.3	22	23.7	95	+− 1.7	±2.85	0.60
Total heterozygous plants.....				731	726.7	238	242.2	969	+− 4.2	±9.09	0.46
38-3	4.06	....	3.94	..	....	37	....	37	....	....	....
38-1	4.11	....	4.57	..	....	12	....	12	....	....	....
38-6	4.14	....	3.75	..	....	41	....	41	....	....	
39-1	4.21	....	3.41	..	....	32	....	32	....	....	
38-16	4.59	....	3.78	..	....	58	....	58	....	....	
40-5	5.29	....	3.64	..	....	91	....	91	....		
Total F_3 plants.....								1,811			

In crosses 13173a and 13174a, density was the only visible differentiating character; hence the separation of the entangling plants depended merely on that character. In series 13172a and 13214a, in which the experimental errors were practically as much on one side as on the other, the error due to entangling was reduced, respectively, by the introduction of the pubescent glume character through the Mealy parent, and by the color of chaff and the beardedness introduced by the Turkey parent. The introduction and consequent segregation of these characters enabled the author to detect the presence of more than one plant, and through their separation the degree of experimental error in these two sets of crosses was greatly lowered.

INFLUENCE OF THE DENSITY OF THE LAX PARENT IN A LAX X COMPACTUM CROSS ON THE DENSITY OF SUCCEEDING GENERATIONS

In connection with table 16 (page 836) the reader perhaps noticed that there was a tendency on the part of some F_1 and F_2 generation frequencies to be shifted somewhat toward the laxer classes while others tended to shift toward the denser classes. Since the dense parent (Dale Gloria) was the same in all seven cases, these variations, if hereditary to any extent, should be ascribed to the influence of lax parents which represent the variable factors.

The mean densities of parent and offspring are represented graphically in figure 80. The curves are arranged in the ascending order of the

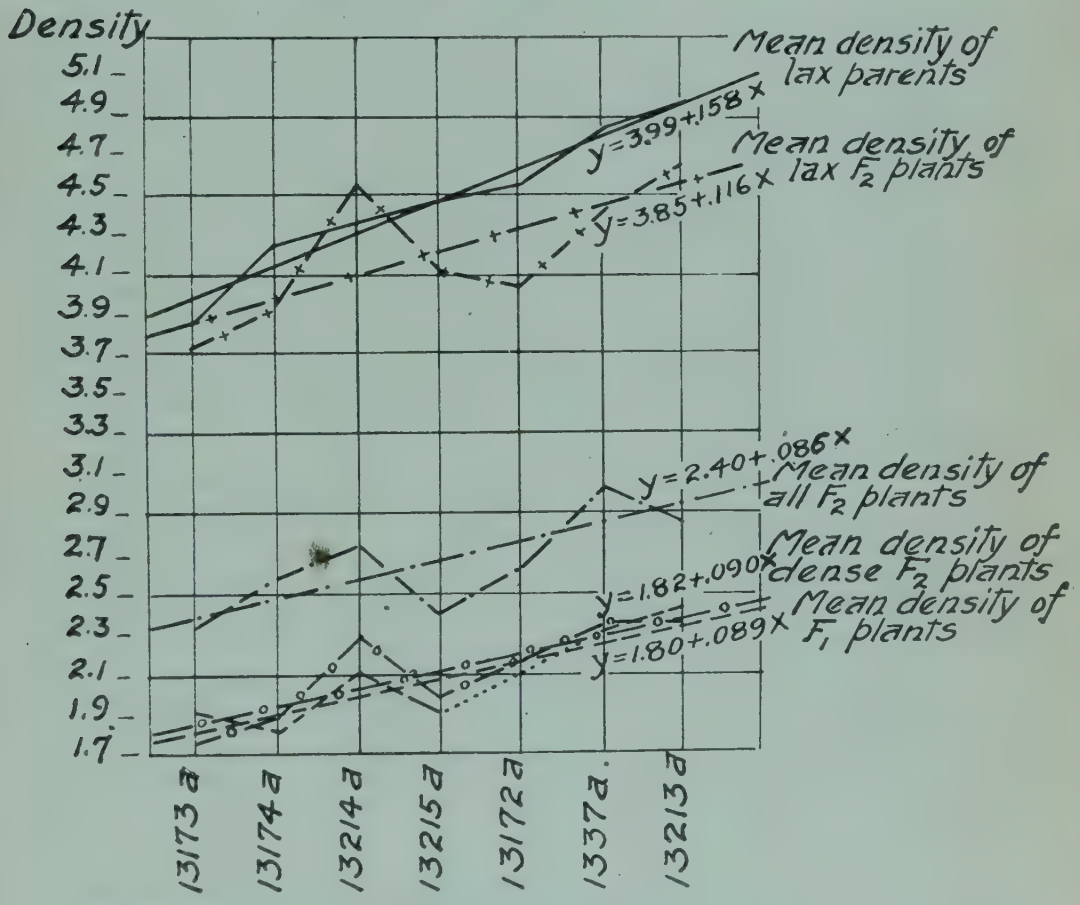

FIG. 80. INFLUENCE OF DENSITY OF LAX PARENT ON DENSITY OF F_1- AND F_2-GENERATION PLANTS

densities of the lax parents. The straight lines fitted to the curves show a general rise; that is, with the increase of the average internode length of the lax parent, the average internode length of the F_1 and the F_2 increase more or less in the same proportion.

The slopes of the fitted lines for the F_1, the total F_2, and the dense F_2 segregate, are practically the same, being 0.089, 0.086, and 0.090, respectively. Those for the lax parents and the lax F_2 segregates show also a general rise but of a higher degree. It should be borne in mind that the higher the class values, the greater is the tendency of the curve toward a higher inclination.

The curves representing the densities of the F_1 and the dense F_2 segregates follow each other very closely. The other curves also follow the same general course. Evidently the material representing the cross with Mealy was somewhat denser, because both the F_1 and the F_2 curve show a similar rise at that point. The rise of the Mealy parent is not in the same proportion.

Aside from these differences, it should be noted that the values of P_1 and F_1 are higher because they represent crops grown in different years and also because they were spaced more widely than the F_2 plants. Besides, the F_1 perhaps shows vigor due to heterozygosis, which, together with increased food supply due to the wide distances between plants, tends to increase the size of the spike without increasing the number of spikelets, which in turn tends to increase the average internode length.

RELATION OF DENSITY OF F_2 PLANTS TO THAT OF THEIR PROGENY

The comparison of the density of F_2 and of F_3 plants leads to the decision as to whether the variations in density, especially of the F_2 heterozygous plants, are hereditary or represent mere fluctuations due to external conditions. To be sure, environmental conditions, as is pointed out in the first part of this paper, have a great influence on the degree of density. The plants used in this experiment were grown on a small area, and consequently the environmental factors had practically as much opportunity to affect the density of one plant as that of another.

In comparing the density of the F_2 plants with that of their progeny, series 13214a may be taken as an example. Deductions based on this cross will apply as well as for the other crosses. The mean densities of

the F_2 parent and the offspring, as shown in table 22, are represented graphically in figure 81. Comparison of the density curves of the F_2 plants with the mean density curves of their progeny shows that, especially in the case of the heterozygous F_2 plants, there is a correlation between the density of the F_2 and that of their F_3 segregates. Since there is such a correlation between F_2 and F_3, these apparent fluctuations are

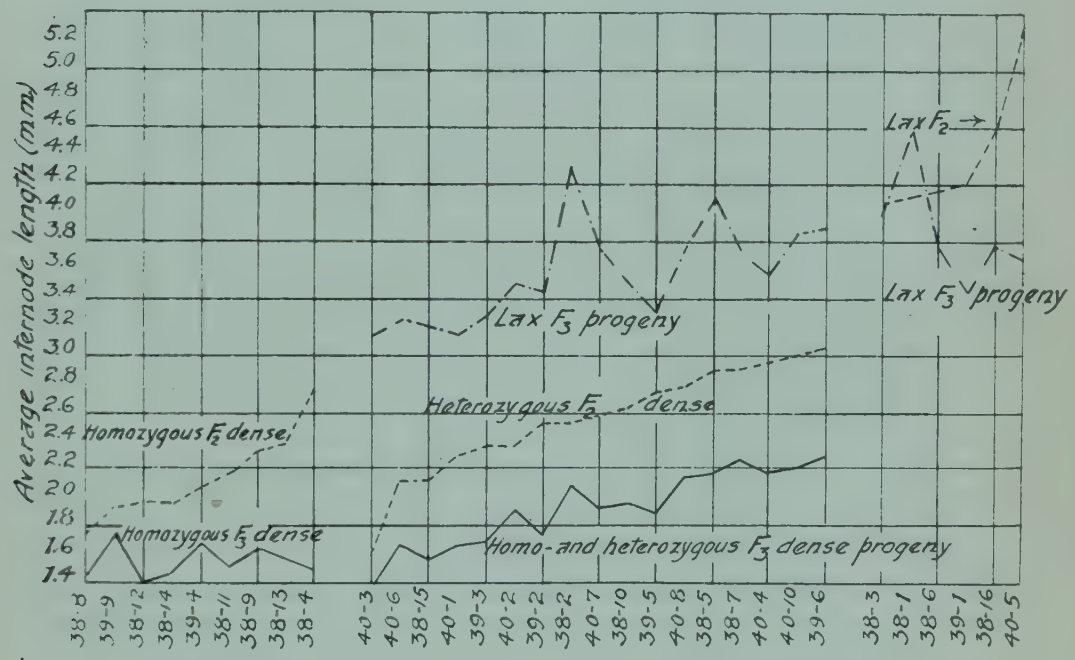

FIG. 81. COMPARISON OF DENSITY OF F_2 WITH THAT OF DENSE (HOMOZYGOUS OR HOMOZYGOUS AND HETEROZYGOUS) AND LAX PROGENY

hereditary variations. It goes without saying, then, that these F_2 heterozygous plants are not genotypically identical with respect to compactness, and that, although all the F_2 heterozygous plants have the general formula *Cc*, they carry besides this factor a group of other factors which tend to increase or decrease compactness.

RELATION OF DENSITY OF DENSE AND LAX SEGREGATES OF HETEROZYGOUS F_2 PLANTS

The presence of factors modifying the degree of density may be further demonstrated by a comparison of the curves of the dense segregates

with those of the lax segregates. This test is made on the assumption that if a group of modifiers is introduced there will be as much chance for these to be transmitted to the dense segregates as for them to be transmitted to the lax forms of the progeny of heterozygous dense F_2 plants; in other words, both dense and lax forms will receive the same dose of modifiers. Accordingly, if a set of modifiers shifts the mean of the dense segregates, say about five classes, toward a plus or a minus direction, the mean of the lax segregates should be shifted likewise, to the extent of as many classes at least, and very likely more, toward the same direction.

On examining the density frequencies shown in tables 23, 24, and 25, it will be noted that whenever the dense segregates of F_2 heterozygous plants are grouped toward the laxer classes the curve of the lax segregates corresponding to them tends also to arrange itself in that direction, and vice versa. For example, in table 23 (series 13214a), of the progeny of 40-3 the dense forms are very dense, with a mean density (table 22) of 1.37. The density of the lax form is 3.18. Comparing this with the progeny of 38-2, the mean of whose dense segregates is 2.08 and of the lax 4.30, it may be seen that whatever interfered with the compactness of the dense plants of 38-2 affected also the density of the lax forms. Throughout tables 23, 24, and 25, in which the details of the frequency distributions are given, the same phenomenon may be observed. The relation between the mean density of the dense segregates and that of the corresponding lax segregates of the F_3 progeny of each heterozygous F_2 plant of series 13214a (table 22) is shown graphically in figure 82. It is seen in these graphs that with the increase or decrease in the density of the dense plants, the density of the lax forms varies in the same direction. This is a direct evidence that besides the density factor there are also modifiers affecting the degree of density within the dense and the lax classes.

GENERAL CONSIDERATION ON THE FREQUENCY DISTRIBUTIONS OF COMPACT X LAX CROSSES

Each dense x lax cross has its own peculiar type of frequency distribution, either in the first or in later generations. The type of distribution seems to depend on the density of the parents concerned and on the

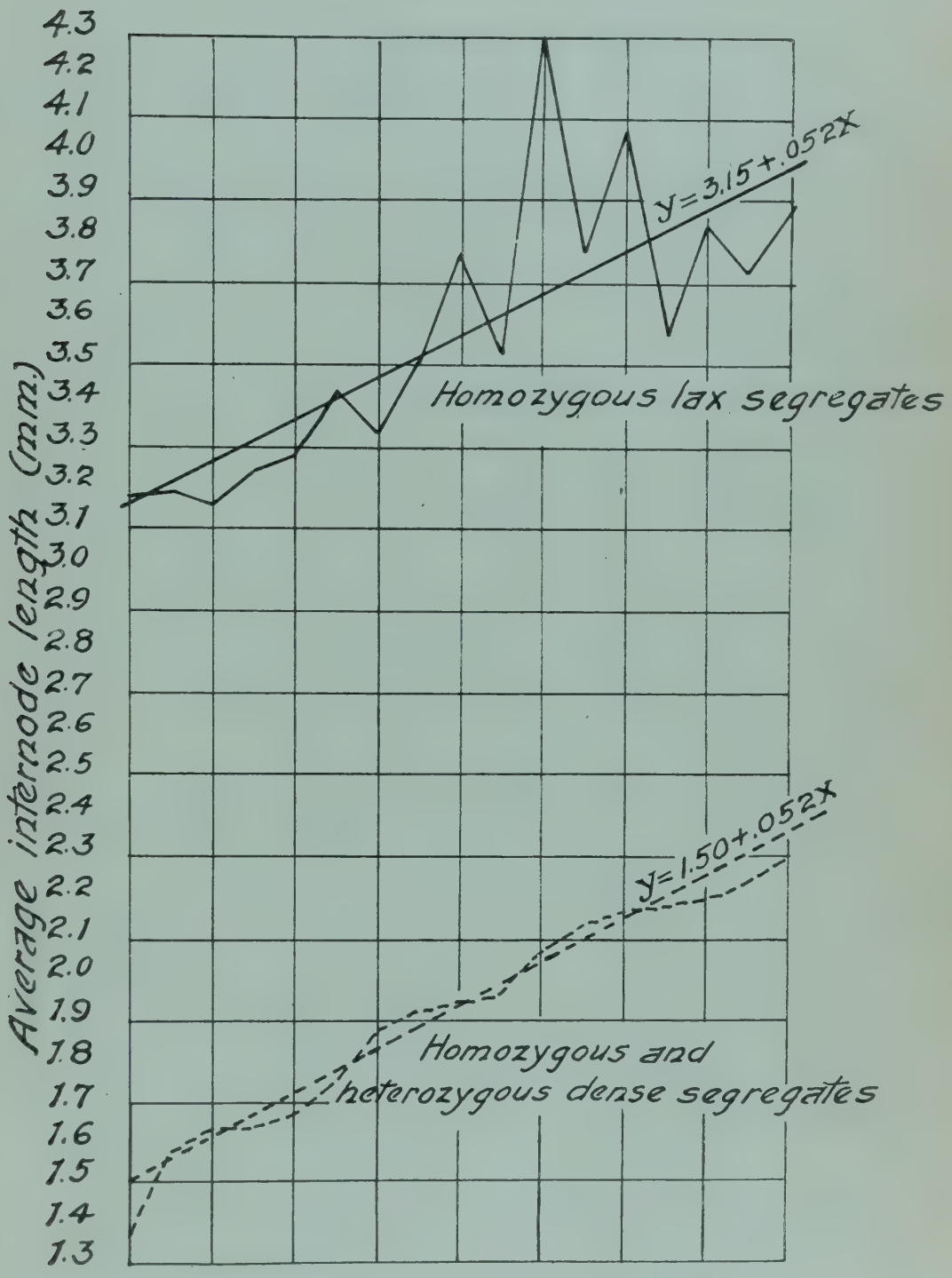

FIG. 82. RELATION OF DENSITY OF DENSE AND LAX SEGREGATES OF HETEROZYGOUS F_2 PLANTS

set of modifying factors introduced by them. In the discussion of table 16 (page 836) it was brought out that lax plants differ from one another in degree of density, and that the density of their progeny varies according to the density of the lax parent, the dense parent being the same. As to the question of modifiers, the frequency-distribution tables 23, 24, and 25 show the characteristics of the curves of each cross.

In series 13214a (table 23), although there is a gap between the dense and lax curves, in a number of cases this gap is not so evident. In figuring out the ratios the determination of the possible line of separation was a matter of judgment in some cases. Series 13172a (table 25) shows a wider gap. To a very small degree the fewness of the plants may account for it. The plants of series 13174a (table 24) show a much wider gap and the presence of two definite curves is at once seen. In crosses between dense and lax forms, all gradations between a distribution such as is shown in series 13174a, and a continuous skew curve, may be obtained.

Crosses made between semi-dense squareheads (often classified as clubs) and lax forms produce an uninterrupted curve which makes it practically impossible to separate them into dense and semi-dense, and lax genetic, classes.

Regarding the mendelian classifications of segregating lines such as those produced by the heterozygous F_2 plants of series 13214a, it will not be out of place to make a few remarks. Some workers on this subject have taken a certain class of density as a dividing line between dense and lax forms, presumably based on the classes of least frequency of the F_2 curve. While such a method may be more or less satisfactory in a cross similar to series 13174a (table 24), it is absolutely unjustifiable in genetic studies and unsuitable for the great majority of crosses in which dense or lax forms appear. In the first place, since F_2 and F_3 plants are grown in different years they do not necessarily show the same degree of density. This is shown in table 23. There is practically no heterozygous plant of the F_3 generation which produced a curve similar to that of the F_2. Theoretically about half of the F_3 curves should have approached the F_2 curve. The reason for this failure lies in the fact that the F_2 plants were grown under more favorable environmental con-

TABLE 23. BEHAVIOR OF DENSITY OF F_2 PLANTS IN F_3. SERIES 13214a, TURKEY x DALE GLORIA

| | | Average internode length (in millimeters) | | |

TABLE 24. BEHAVIOR OF DENSITY OF F_2 PLANTS IN F_3. SERIES 13174a, EXTRA EARLY WINDSOR x DALE GLORIA

| | | Average internode length (in millimeters) | | |

TABLE 25. BEHAVIOR OF DENSITY OF F_2 PLANTS IN F_3. SERIES 13172a, MEALY x DALE GLORIA

| | | Average internode length (in millimeters) | | |

ditions than were the F_2. Now if, for example, density class 3.2 based on the F_2 curve (table 23) is taken as the dividing line and is used for separating the dense and lax forms of the F_3, it will be noticed that a large number of lax forms of the F_3 will be included in the dense class.

It has been mentioned that each F_3 curve has its peculiar mode of distribution. In tables 23 and 25 it is shown that the frequencies of some dense curves extend beyond the classes where the curves of some lax forms have begun. The peculiarity of each curve necessitates the taking of each curve and the separation of the dense from the lax forms at the class or the probable class of least frequency. If the density curves of segregating forms are not prepared, more trustworthy results can be obtained by classifying the forms by eye than by taking an arbitrary dividing line. This latter method can be used in cases in which the variations are discontinuous.

In specices crosses, discontinuous curves are the exception rather than the rule, and separation of dense and lax forms into two genetic classes by an arbitrary dividing line has no meaning because such a separation cannot be made even by the examination of the curves, even disregarding the fact that some specific forms which carry the density factor may be laxer than most of the *vulgare* forms.

That density is a dominant character and is inherited in the 3:1 ratio has been shown by Spillman (1902), Strampelli (1907), Wilson (1907), Von Tchermak (1910), Nilsson-Ehle (1911), Mall (1912), Parker (1914), and others. The three last-named have called attention to the fact that forms laxer and denser than the parental types are obtained also in *compactum* x *vulgare* crosses.

The use of the word *squarehead* for semi-dense forms by some authors accounts for the disagreement of their results. Von Rümker (1909) obtained from compact x non-compact crosses, compact, squarehead, and *vulgare* forms in approximately the ratio 1:2:1. No doubt the "squareheads," which proved to be heterozygous, were heterozygous club forms. Von Rümker cites another case in which the F_2 segregated into dense and lax forms approximating 3:1, there being no squarehead forms. The heterozygous forms in this cross could not be distinguished from dense forms.

Biffen's (1905) results, which are often cited as contrary to those obtained by others, seem rather to agree with Von Rümker's. Such differences as exist are due to methods and nomenclature. Biffen crossed Squarehead's Master with Red King, the average internode lengths being, respectively, 3.2 and 4.6 millimeters. The F_1 hybrid ears averaged 4.8 millimeters in internode length, and the F_2 ranged from 3.2 to 5 millimeters. In this early work the frequencies are not given, but it appears that the distribution was of the normal, or skew, type. Using 4.6 (the mean of Red King, or the internode length of this lax parent) as the dividing line, Biffen found that 78 plants were laxer than the lax parent and 22 were intermediate between the dense and the lax parent, while there was no form denser than Squarehead's Master. From this result Biffen concluded that in this case laxness was dominant. In the first place, Squarehead's Master, with an internode length of 3.2, does not fall in the *compactum* class and the cross should not be included in that category. In the second place, the use of the density of the lax parent as the dividing line seems to be too arbitrary and unjustifiable from a genetic standpoint.

Neither does Biffen's Rivet x Polish cross fall in this category, since it does not belong to the *sativum* group. In crosses of this type specific segregations occur which greatly complicate ratios. His Devon x Hedgehog cross is of the semi-dense *compactum* x lax type. The photographs shown in the article cited, and also by Bateson (1909:23), show that the F_1 is intermediate dense and the F_2 evidently approximates the 3:1 ratio, the heterozygous forms being slightly laxer than the dense parent.

Biffen's results, then, so far as the *compactum* x lax cross is concerned, may be regarded as being in accord with similar work done by others.

Since different types of dense and lax forms have been used by various investigators, their results with respect to degree of density have been different. Segregation into two distinct curves is obtained as the degree of density of the parents approaches the extremes of the dense and lax classes. As a rule, the closer the parents approach in degree of density, the more continuous the curves will be. This statement applies for crosses made within the *sativum* group. The existence of several factors producing varying degrees of density is evident.

THE NATURE OF DENSITY FACTORS

Three questions of special interest arise, regarding the nature of the density factors producing varying degrees of density in so-called pure lines. They are: (1) Is the density of the *compactum* type caused by but one factor pair, and are the degrees of density produced by the presence of modifiers? (2) Do the forms varying in degree of density carry different density factors allelomorphic to one another, or (3) Are they caused by multiple factors?

A considerable amount of work has yet to be done to answer these questions definitely, as numerous genetic analyses are necessary. A few suggestions based on experiimental results can be made, however, regarding the probable nature of these density factors.

The results of all the *compactum* x lax crosses reported thus far show the presence of but one density factor; a 15:1 ratio has not yet been obtained. But in crossing a *compactum* with a somewhat dense *vulgare*, not infrequently forms are obtained which are laxer than the *vulgare* and denser than the *compactum* parent. For the sake of simplicity in previous discussions, this occurrence was ascribed to the presence of modifiers. The writer believes that these modifiers are secondary factors representing varying degrees of density. The factorial combinations according to this hypothesis, and their corresponding phenotypes, may be illustrated in the following manner:

P_1	CC dd x cc DD *compactum* slightly dense *vulgare*							
F_1	CcDd *compactum* slightly laxer than dense parent							
F_2	1 CCDD 2 CCDd	1 CCdd 2 CcDD	2 Ccdd 4 CcDd	1 ccDD	2 ccDd	1 ccdd		
	12 *compactum*			4 *vulgare*				
	3 denser than dense parent	3 approximately of same density as dense parent	6 laxer than dense parent	1 same as *vulgare* parent	2 slightly laxer than *vulgare* parent	1 much laxer than *vulgare* parent		

In the preceding outline, *C* stands for the high degree of compactness introduced by the *compactum* parent, and *D* for the slight degree of compactness exhibited by the *vulgare* parent. This hypothesis accounts for the production of stable forms *CCDD* denser than the *compactum* parent and *ccdd* laxer than the *vulgare* parent.

In instances in which lax stable forms somewhat denser than the lax parent appear, the phenomenon may be explained according to the same hypothesis. If the above extreme dense *CCDD* and lax *ccdd* forms taken as parents are crossed, stable forms denser than *ccdd* will be obtained according to the factorial combinations.

If there are different factors of density producing the *compactum* type, certain crosses between two *compactum* forms should give 1 in 16 or 1 in 64 lax forms. Let it be supposed that the *compactum* parents have the genotypic forms $C_1C_1c_2c_2$ and $c_1c_1C_2C_2$ where there are two different *C* factors. With two factor differences, one plant out of sixteen in the F_2 should have the $c_1c_1c_2c_2$ constitution, therefore being very lax. The writer knows of but one cross between two club forms, and from that cross, among 130 F_2 plants no lax forms were observed, although considerable variations were found within the dense classes. In this case both parents seemed to be homozygous for the same *C* factor; and the *C* factors contributed by both parents either were identical or belonged to the same allelomorphic series.

The author has evidence that the density factor of the *compactum* type may belong to a multiple series. The Black Bearded Spelt carries a density factor which may be isolated by crossing it with a lax *vulgare* form. About three-fourths to one-half of the F_2 *vulgare* forms are dense and semi-dense. In five such crosses the results have been similar. This shows that a *C* factor is carried by this particular spelt. If this factor is identical or forms an allelomorphic series with another *C* factor, the F_2 *sativums* segregating in a cross between this spelt and a club should be all dense. The fact that in such a cross lax *sativum* forms also are occasionally obtained, shows that in this case there were two distinct *C* factors involved.

Another *C* factor is carried by the *dicoccum* form known as Black Winter Emmer. When this form is crossed with a *vulgare* it throws

a certain proportion of distinctly dense *sativum* individuals. The F_2 plants from eight such crosses were examined and compact forms were recorded in every case. As in the preceding instance, in the F_2 derived from two Black Winter Emmer x club crosses, consisting of about 150 F_2 individuals, soft lax vulgare types could be counted, although most of the *sativum* types were dense. Here again it appears that, as in the preceding cross, two different non-allelomorphic multiple *C* factors were introduced.

Summarizing the foregoing discussion, it is apparent that:

1. There are density factors each producing shortening of the rachis internode in different degrees. These may be present in addition to the *compactum* factor.

2. There is as yet no sufficient evidence that some *compactum* factors may form an allelomorphic series. Neither is there any evidence that such series may not exist.

3. There exists in wheat more than one density factor belonging to multiple series. If such multiple density factors are present, eventually 15 : 1, 63 : 1, and other ratios will be obtained from *compactum* x *vulgare* crosses.

FACTORS PRODUCING SQUAREHEADEDNESS AS COMPRISING ONE OF THE GROUP OF FACTORS MODIFYING DEGREE OF DENSITY

A modifier, as generally held, may be a factor affecting a particular character quantitatively, the presence of which is detected from the degree of modification of the character which it modifies. In a broad sense, however, any factor or character whose presence affects or even inhibits more or less the expression of another character should be regarded as a modifier.

The irregularities among the F_2 density curves of dense x lax crosses shown in this study were ascribed to the presence of modifiers, as the genetic analyses applied to the crosses showed conclusively the presence of but one density factor. Proofs that these variations were hereditary, and not caused by environmental conditions, were also given.

The nature of one of these modifiers, the character for squareheadedness, may here be considered. In crosses in which a non-squarehead was involved, it was noticed that there was an independent segregation of

density and squareheadedness, and that whenever the latter character was present, whether the plant was dense or lax, there was, as a rule, a reduction of the average internode length.

Density notes derived from series 13172a are summarized in table 26. This cross, it will be recalled, is between Mealy, a lax non-squarehead,

TABLE 26. MEAN DENSITY OF F_3 LAX PLANTS CLASSIFIED ACCORDING TO PROPORTION OF SQUAREHEADS AND VULGARE FORMS. SERIES 13172a

All squareheads		More squareheads than *vulgare*		Squareheads = *vulgare*		More *vulgare* than squareheads		All *vulgare*	
Pedigree	Density	Pedigree	Density	Pedigree	Density	Pedigree	Density	Pedigree	Density
30-19	3.00	29-1	3.15	29-3	3.30	29-5	3.65	29-2	3.64
30-22	3.12	29-6	3.06	....	....	29-14	4.26	29-7	4.08
..	....	29-13	3.88	....	....	30-1	4.23	29-10	3.70
..	....	30-6	3.41	....	....	30-8	3.56	29-11	3.69
..	....	30-7	3.08	....	....	30-10	3.52	29-12	4.03
..	....	30-9	3.01	....	....	30-16	3.39	30-3	3.53
..	....	30-12	3.36	....	....	30-17	3.43	30-4	3.56
..	....	30-13	3.33	....	....	....	....	30-15	3.47
..	....	....	....	....	....	....	....	30-20	3.64
Mean and average error	3.06±0.04		3.28±0.07		3.30		3.72±0.11		3.71±0.05

and Dale Gloria, a dense squarehead. In this cross both density and squareheadedness segregated independently. The table shows the density of the lax forms of the F_3-generation lines arranged in five classes, according to the observed proportions of squareheads to non-squareheads. In the first class are included the F_3 plants which consisted of squareheads only; the second class includes the pedigrees that produced more squareheads than *vulgare* forms; the other three classes represent progenies consisting of an equal number of these two forms, of an excess of *vulgare*, and of only *vulgare*, respectively.

By averaging the degree of density of each group it is found that the average internode length increases inversely with the proportion of squareheads. The average internode length of the squareheads was 3.06 ± 0.04, while that of the plants producing an excess of squareheads was 3.28 ± 0.07. The densities of the class yielding more *vulgare* than squareheads and that producing only *vulgare* were 3.72 ± 0.11 and 3.71 ± 0.05, respectively. The difference in the average internode length of the extreme classes was 0.65 ± 0.06. Comparison in terms of the average of the means of these two classes, shows this difference be-

tween the density of pure squareheads and that of pure *vulgare* to be equal to about 20 per cent of their means, which is rather remarkable.

Were the lax plants of the F_3 generation all or practically all squareheads, one would expect the elimination of variations as great as those found in the crosses between *vulgare* and dense squareheads. Series 13174a (table 24, page 850), which represents a cross between a squarehead and a dense squarehead, shows the absence of shifting of the curves back and forth, so evident in tables 23 and 25, which represent dense squarehead x *vulgare* crosses.

Although the variations introduced by the presence of both *vulgare* and squarehead forms is eliminated in cross 13174a (table 24), other modifiers must be present because the curves still show inheritable variations. The nature of these remaining modifiers is not as yet known.

It is not difficult to explain how squareheadedness increases density. Physiological studies show that squareheadedness, which is brought about by the shortening of the terminal internodes, is due to contact and pressure caused by the differential rate of growth of parts of the plant surrounding the spike during its earlier periods of growth. If, during the process, the terminal internodes fail to attain their normal size, that part of the head will be denser than it would have been if the plants were allowed to grow normally. This shortening of internodes of the terminal part of the head is the direct cause of the decrease of the average internode length of the entire head.

RELATION OF SQUAREHEADEDNESS TO DENSITY IN F_2-GENERATION PLANTS

The modes of inheritance of squareheadedness and of density have been discussed separately herein. It is necessary now to illustrate the relation between these two characters in crosses in which both of these characters have been introduced. Series 13172a, 13214a, 1337a, and 13173a (tables 27, 28, 29, and 30, respectively), which have already been considered, will be used again as examples, because each illustrates a different mode of inheritance.

Before examining the behavior of the F_2 plants, the distribution of the parent plants with respect to density and squareheadedness may be reconsidered. This distribution, although based on few numbers, is shown graphically in figure 83. The plants recorded do not represent samples of

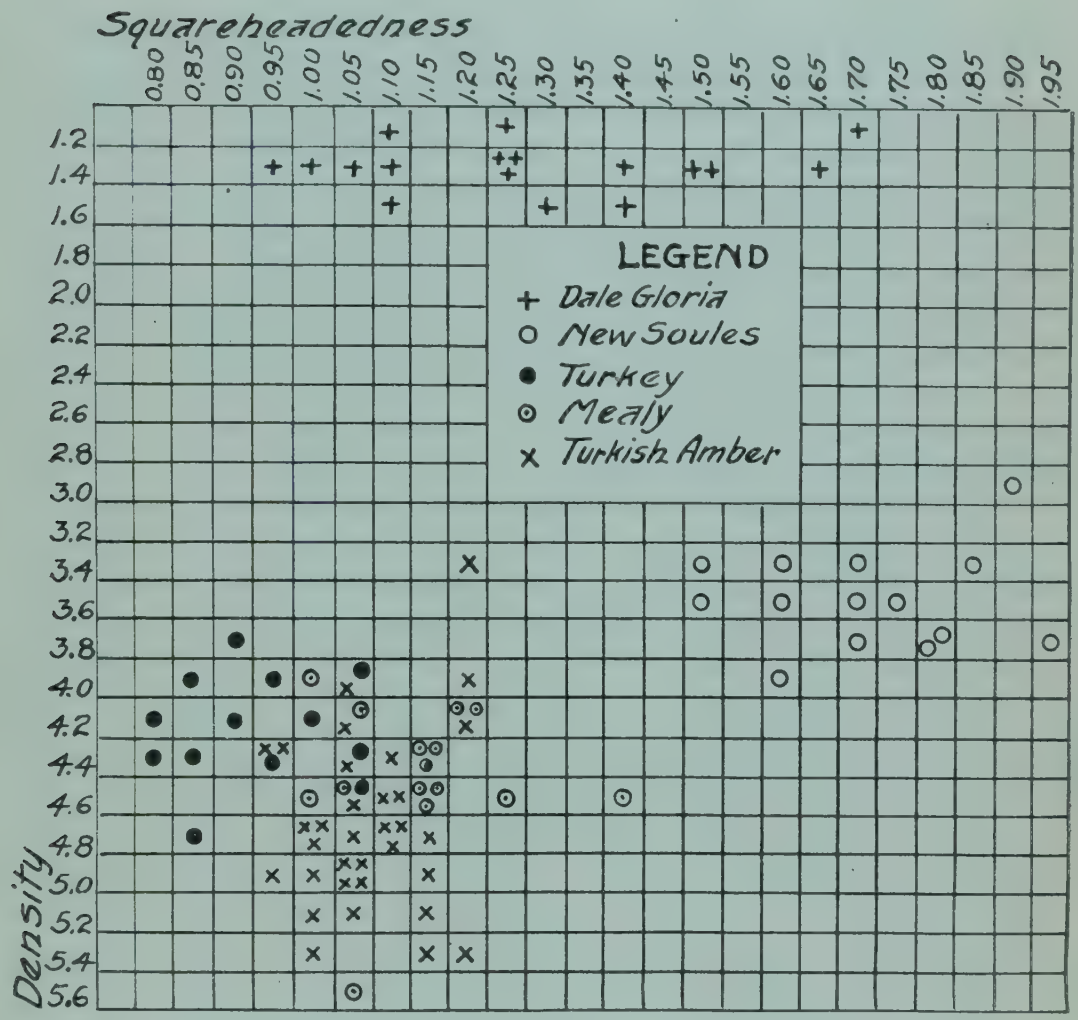

FIG. 83. DISTRIBUTION OF PARENTAL PLANTS WITH RESPECT TO DENSITY AND SQUAREHEADEDNESS

the varieties used in making the crosses; they are the progeny of each of the plants used as parents.

Dale Gloria, it is seen, is distributed within a very narrow range with respect to density, but within a wide range with respect to squareheadedness. This latter range does not represent the genotypic range of the variety, if one may be allowed to use that expression. The length of the rachis itself is about 2 to 3 centimeters. If the terminal spikelets are ster-

ile, as often happens in dense clubs and less frequently in lax forms, this sterility and rudimentary condition will keep the terminal rachis internodes from developing further while the other internodes continue their growth. A head of this type will have a high coefficient of squareheadedness. If, on the contrary, the terminal florets develop vigorously, the increase in the size of the grain will tend to stretch the internodes somewhat. With a vigorous growth of the grain is associated a relative growth of the adjacent internodes, and with as short a head as that of the club in question it does not take much increase in internode length to lower the squareheadedness of some individuals down to classes 1.00 to 1.25.

The distribution of New Soules is entirely different from those of the other lax plants used in the crosses. It is somewhat more toward the denser classes and falls distinctly within the squarehead classes.

Turkish Amber is a *vulgare*, but its average internode length is greater than that of any other of the forms represented.

TABLE 27. RELATION OF SQUAREHEADEDNESS TO DENSITY IN F_2 SEGREGATES. SERIES 13172a, MEALY x DALE GLORIA

(Mean dense plants, D=2.01, Sq.=1.34; mean lax plants, D=3.95, Sq.=1.23)

Density	Squareheadedness																			
	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75
1.5					1					1	1	1					1		
1.7								1				2	2		2	1			
1.9						1			1		1		1		2	1			
2.1					1			3	4	1		3	1	1		1			1
2.3		1			1	1			1		1			1		1			
2.5							1	1	2	2		1		1	1				
2.7							2	1											
2.9						1													
3.1																			
3.3								1						1					
3.5											1								
3.7				1						1	1								
3.9								2					1		1				
4.1					1					1									
4.3					1														1
4.5		1	1																
4.7				1	1			1				1							

Mealy has practically the same distribution as Turkish Amber but is somewhat less lax.

Turkey is the least lax in the *vulgare* group and is located very much toward the non-squarehead classes.

The mode of inheritance which might generally be expected in *compactum* x *vulgare* crosses is that of the Mealy x Dale Gloria series (table 27), which shows a wide range of distribution with respect to squareheadedness. Theoretically, since Dale Gloria carries the factors responsible for squareheadedness and Mealy does not, both density and squareheadedness would be expected to segregate independently, which happens in this case. Using, for practical purposes, class 1.30 or 1.35 as a dividing line, it is seen that there are about as many individuals on the side of squareheadedness as on the side of non-squareheads. By using as a guide the distribution of the Mealy parent shown in figure 83, it becomes very evident that in this cross the character of squareheadedness has been introduced among the non-squareheads. The mean value of squareheadedness of the lax parent is 1.14 and that of the lax plants of the cross is 1.23, showing an increase of 0.09. While out of 15 Mealy parental plants (figure 83) there was but one individual in the squarehead classes in the F_2 generation, out of a total of 20 plants there were about four or five times more individuals in these classes. In table 26, which represents the same cross, it has been shown that some of these lax squareheads remained stable.

The distribution when Turkey was the lax parent (table 28) was strikingly different from that in the case of Mealy. In the Turkey x Dale Gloria cross, no lax squareheads appeared.

On comparing the dense classes of tables 27 and 28 with respect to their squareheadedness distribution, it is seen that the entire distribution has been shifted to the left in the latter table. The mean squareheadedness of Dale Gloria is 1.28; that of the dense plants of the cross is 1.17, showing a shifting of 0.11 toward the non-squarehead classes. While the squåreheadedness of the dense form is affected by that of the lax forms, the difference in the coefficients of the lax parent and the lax segregates, these being 0.92 and 1.00, shows that the lax segregates are in turn influenced to some extent by the squareheadedness of the dense parent.

TABLE 28. RELATION OF SQUAREHEADEDNESS TO DENSITY IN F_2 SEGREGATES. SERIES 13214a, TURKEY x DALE GLORIA

(Mean dense plants, D=2.18, Sq.=1.17; mean lax plants, D=4.23, Sq.=1.00)

Density	Squareheadedness														
	0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50
1.5															1
1.7				1	1	1			2			1	1		
1.9				1					1		1	2			
2.1								1	1	2	2			1	
2.3						1			1	1	2				1
2.5					4	1		3	3					1	
2.7			2	1	1			1			1			1	
2.9			1			4									
3.1						2									
3.3															
3.5															
3.7															
3.9															
4.1	1					1			1						
4.3			1		1										
4.5					2		2								
4.7				1											
4.9			1		1										
5.1															
5.2					1										

In the cross in which Turkish Amber was used (table 29), the squareheadedness of the lax segregates occupies practically the same position as that of the lax parent itself, the values of squareheadedness of the lax parent and the lax segregates being 1.04 and 1.07, respectively. This slight shifting toward the non-squarehead classes may well be disregarded. Unlike the condition in the preceding cases, the dense forms showed no visible effect of the lax parent. The mean squareheadedness of the dense segregates, instead of being less, was slightly greater than that of the dense parent and practically the same as in series 13172a.

In the fourth cross (table 30) the lax parent was New Soules, a distinct squarehead. The lax segregates of this cross were all squareheads, and with regard to density they occupied the same position as the lax squarehead parent (figure 83).

Incidentally it should be noted from this table that, while the range

TABLE 29. RELATION OF SQUAREHEADEDNESS TO DENSITY IN F_2 SEGREGATES. SERIES 1337a, TURKISH AMBER x DALE GLORIA

(Mean dense plants, D=2.23, Sq.=1.35; mean lax plants, D=4.30, Sq.=1.07)

Density	Squareheadedness																			
	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80
1.5						1													
1.7								1											
1.9						1	1	4			1	1	1						1
2.1					1	1	1	1		1			1		1				
2.3					1			1	1	1		2	1	1					
2.5								1	1	1	1						1		
2.7										2									
2.9					1	1	1			1	1								
3.1													1	1	1				
3.3																			
3.5																			
3.7					1														
3.9			1		1						1								
4.1	1			1	1				1										
4.3		1		1	1	1													
4.5	1		1	2				1											
4.7				2															
4.9			1																
5.1																			
5.3																			
5.5			2																

of density of the dense segregates of other crosses extends as far down as class 3.1, that of this cross (table 30) is confined within classes 1.3 to 2.1 with but one individual in class 2.5. This difference is accounted for by the higher degree of density of New Soules (figure 83) as compared with those of the other lax forms.

Recapitulating the points of interest brought out in the discussion of these four tables, the following general deductions can be made:

1. The factors of density and those of squareheadedness are totally independent of each other. They segregate and recombine independently.

2. The wheat varieties of the *sativum* group have different degrees of density and of squareheadedness. Even among the *vulgare* plants this latter form of compactness, as measured by its coefficient, varies. In

TABLE 30. RELATION OF SQUAREHEADEDNESS TO DENSITY IN F_2 SEGREGATES. SERIES 13173a, NEW SOULES x DALE GLORIA

(Mean dense plants, D=1.64, Sq.=1.43; mean lax plants, D=3.64, Sq.=1.59)

Density \ Squareheadedness	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85
1.3	1				1											
1.5	1					2		1	1						1	1
1.7	2			1	1	1	1		1		1			1	1	
1.9			1	1	1		2	1								
2.1						1	1		1		1			2		
2.3																
2.5						1										
2.7																
2.9										1						
3.1																
3.3											1	1				
3.5												1	1			
3.7							1									
3.9								1								
4.1								1								
4.3																1

crosses in which one parent is the same, not all *vulgare* nor all squareheads nor all dense forms produce a frequency distribution of squareheadedness or of density of the same type and within the same range. Whether the range will remain approximately in the same location, or will shift one way or the other, is determined to a great extent by the degree of squareheadedness or of density of the different forms of *vulgare* or squareheads, as the case may be, which are involved in the cross.

3. There are exceptions to the general rule stated above. In series 1337a there was a visible segregation of density but not of squareheadedness. In this case there was evidently interference by another factor.

Nilsson-Ehle (1911) considers the inheritance of squareheadedness and gives a factorial explanation to account for the apparent proportion in which it appeared in some of his crosses. But, while Nilsson-Ehle used the term *squarehead* for lax forms—which have a comparatively shorter average internode length than the *vulgare* forms—that term is applied in the present paper to forms showing a relative density of the

middle and the upper third of the spike of about 1.33 or over, irrespective of the average internode length. It is not possible to compare Nilsson-Ehle's results and hypothesis with those from this study.

RELATION OF LENGTH OF RACHIS TO DENSITY IN HYBRID PLANTS

Length of rachis is dependent on two factors, namely, the number of internodes and their length. If the number of internodes in a population is more or less constant, as has been the case in all the crosses between Dale Gloria and other forms considered herein, the length of the rachis is directly proportional to the average internode length. This is so obvious that it needs no illustration.

If both factors are made variable by the selection of parents which vary both in number and in length of internodes, then there is no correlation between length and density. As an illustration a cross may be cited which was made by the writer for this purpose. This cross was Silver Club x *Aegilops ovata*. Silver Club (Plate LXVII, upper, 3) is a club wheat from four to five centimeters long, with about seventeen to twenty internodes. The Aegilops (Plate LXVII, upper, 1) also was short, like the club wheat, but had only six internodes of an average length of about six to seven millimeters. The basal internodes were the shorter, their spikelets being rudimentary.

Unlike the parents, the F_1 plants all had long heads, resembling the spelt wheat. Three plants obtained in the F_2 also were lax. The point of interest in this cross was that the F_1 and F_2 plants did not inherit length of rachis from their parents, but number and length of internodes. The F_1 heads usually had from twelve to fourteen internodes from six- to seven millimeters in length. The three F_2 plants showed some variation in length. In the F_1 plants, both characters being intermediate, the heads were necessarily much longer than in either parent. It would be expected, if sufficient F_2 plants were obtainable, that the plants would segregate with respect to both characters into short heads dense and lax, that is, with many and with few internodes, and also comparatively long heads dense and lax, with possible intermediate forms.

In this connection it may be pointed out that what has been called vigor due to heterosis in wheat is often the appearance of unusually long heads in F_1 or later generations in crosses with certain emmers.

These are, as a rule, somewhat dense and bear some thirty internodes to the spike. Hence the question is rather one of number of internodes and internode length. The plants that combine the internode length of the *vulgare* parent with the number of internodes of the emmer must necessarily be unusually long.

In actual practice, in a cross such as the above a considerable number of synthetic spelts appear. These spelts have the peculiarity, as is shown later, of producing internodes longer than those of the lax parent. The appearance of this new type helps to increase the proportion of unusually long heads.

RELATION OF LENGTH OF CULM TO RACHIS LENGTH AND DENSITY

In a pure line of wheat there is practically no correlation between culm length and density, but there is a correlation between culm length and length of rachis. The plant that produces a short culm due to unfavorable environmental conditions naturally produces a small head; but such a head as a rule has fewer rachis internodes than the mean of the line, and therefore, although the undeveloped head is short, its density has not been affected to any extent because the number of rachis internodes has decreased more or less proportionately.

The writer's studies of the relation of culm length to density were made on series 13214a, because this line produced practically no squareheads. Squareheading, it has been shown, unless it is due to favorable growth conditions, has a tendency to shorten the average rachis internode length. There being no squareheads in the material used, that factor was eliminated.

The question of the relation of culm length to other characters of the head is of interest from both the economic and the genetic viewpoint. Because of the many phases to which this problem of density has led, it was not possible in this investigation to study the relation of culm characters as intensively and extensively as the subject deserves. Sufficient data have been obtained, however, to give an idea of the general behavior of this character.

Due to the great variability of culm length, the preliminary studies were made with a number of progenies of F_2 plants each of which had yielded on an average about 60 individuals. The frequencies of the

TABLE 31. Relation between Culm Length, Rachis Length, and Average Internode Length

Culm length (centimeters)'		59	61	63	65	67	69	71	73	75	77	79	81	83	85	87	89	91	93	95	97	99	101	103	105	107	109	111	Number of plants	Mean
Rachis length (centimeters)		1.8	2.2	2.6	3.0	3.4	3.8	4.2	4.6	5.0	5.4	5.8	6.2	6.6	7.0	7.4	7.8	8.2	8.6	9.0	9.4	9.8	10 2	10.6	11.0	11.4	11.8	12.2		
Average internode length (millimeters)		0.9	1.1	1.3	1.5	1.7	1.9	2.1	2.3	2.5	2.7	2.9	3.1	3.3	3.5	3.7	3.9	4.1	4.3	4.5	4.7	4.9	5.1	5.3	5.5	5.7	5.9	6.1		
Pedigree																														
38-3	Culm	..	..	..	..	1	..	..	1	..	5	1	..	8	2	3	4	2	5	2	..	2	2	2	..	..	..	..	40	87.44
	Rachis	..	..	..	..	..	..	..	..	..	1	..	1	1	5	3	5	9	5	5	2	1	1	1	..	..	..	..	40	8 14
	Av. internode	..	..	..	..	..	..	..	1	..	..	..	..	2	5	5	3	8	5	3	3	2	..	..	..	..	..	..	37	4 01
38-4	Culm	2	3	3	3	3	9	10	5	4	2	..	..	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	46	69.52
	Rachis	..	..	14	19	8	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	46	3 03
	Av. internode	..	..	7	24	11	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	44	1 52
38-5	Culm	..	..	..	..	..	1	5	3	5	1	2	4	4	2	3	2	1	..	1	..	..	..	..	..	..	..	..	34	79.53
	Rachis	..	..	..	..	3	4	5	4	5	5	3	3	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	34	4 91
	Av. internode	..	..	..	..	3	5	4	5	3	..	3	..	..	..	1	..	5	2	1	..	..	..	..	..	..	..	..	32	2 75
38-6	Culm	..	..	1	..	..	2	1	4	2	1	4	1	4	4	6	1	3	1	4	1	1	..	1	..	..	..	..	42	83 71
	Rachis	..	..	..	..	..	..	..	..	..	1	1	3	4	5	4	1	6	5	3	5	..	3	..	1	..	..	..	42	8 01
	Av. internode	..	..	..	..	..	..	..	..	..	..	1	2	3	4	14	8	3	..	3	3	..	..	..	..	..	..	..	41	3.80
38-7	Culm	1	..	..	..	1	1	5	6	4	7	8	2	6	4	2	4	4	4	1	2	1	..	..	..	..	..	..	63	81 16
	Rachis	..	..	..	1	4	2	11	9	12	4	6	4	2	..	2	..	1	..	1	3	1	..	..	..	..	..	..	63	5 36
	Av. internode	..	..	..	..	5	6	4	12	14	4	2	1	2	3	1	2	1	2	1	..	..	..	..	..	..	..	..	60	2.61
38-8	Culm	1	2	1	5	6	9	7	6	7	2	5	7	5	5	3	..	..	1	..	..	..	..	..	..	..	..	..	72	75 53
	Rachis	..	5	13	27	25	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	72	3 05
	Av. internode	..	3	12	38	14	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	69	1 51
38-9	Culm	..	1	..	4	1	4	8	7	11	10	8	8	6	9	5	..	1	1	1	..	..	..	..	..	..	..	..	85	77.59
	Rachis	..	1	5	18	29	20	11	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	85	3.47
	Av. internode	..	1	5	22	37	15	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	83	1.66
38-10	Culm	1	..	..	..	1	..	1	1	1	2	3	1	4	4	2	1	5	5	2	3	2	2	..	1	..	..	..	42	87.09
	Rachis	..	..	..	4	3	6	5	7	3	5	1	..	1	..	6	..	..	..	..	1	..	..	..	..	..	..	..	42	4 91
	Av. internode	..	..	..	3	7	3	7	9	1	..	..	1	3	1	2	3	..	..	..	..	..	..	..	..	..	..	..	40	2 39
38-16	Culm	..	..	..	..	..	..	..	..	..	..	1	3	4	1	7	3	6	6	5	5	4	3	1	2	2	2	2	57	93 77
	Rachis	..	..	..	..	..	..	..	..	..	..	4	3	..	8	5	14	5	4	5	4	1	2	1	..	1	..	..	57	7 97
	Av. internode	..	..	..	..	..	..	..	..	..	..	3	1	6	10	8	8	10	8	2	1	..	..	..	1	..	..	..	58	3.83
40-4	Culm	..	..	..	..	..	..	1	2	..	1	..	1	2	3	4	4	5	7	8	6	5	7	3	3	1	1	..	64	93.59
	Rachis	..	..	..	1	3	9	12	8	10	7	..	2	1	4	3	2	2	..	..	..	..	..	..	..	..	..	..	64	5 06
	Av. internode	..	..	..	..	5	7	8	12	14	1	1	1	2	4	2	2	2	..	..	..	..	..	..	..	..	..	..	61	2 52
40-5	Culm	..	..	..	..	..	..	..	1	..	3	..	8	4	7	7	4	12	9	4	4	10	6	6	3	3	1	1	93	92.59
	Rachis	..	..	..	..	..	1	..	..	1	11	7	9	13	15	9	6	5	11	..	3	2	1	..	..	..	..	..	94	7.05
	Av. internode	..	..	..	..	..	..	..	..	..	1	1	3	15	23	14	17	7	7	2	..	..	1	..	..	..	..	..	91	3.69
40-6	Culm	..	..	..	..	..	..	..	2	2	5	3	4	7	8	4	9	3	4	3	1	1	..	..	..	..	..	..	56	85 32
	Rachis	..	..	7	10	9	12	7	3	..	2	2	..	1	..	..	1	1	1	..	..	..	..	..	..	..	..	..	56	3.95
	Av. internode	..	..	7	8	15	11	5	1	1	1	..	1	2	..	3	..	..	..	..	..	..	..	..	..	..	..	..	55	1 93
40-7	Culm	..	1	..	3	4	..	6	4	3	..	7	6	5	6	2	4	2	1	2	1	..	..	..	..	..	..	..	57	78 92
	Rachis	..	..	2	2	8	7	10	5	7	6	..	1	1	1	2	..	1	..	2	..	..	..	..	..	..	..	..	55	4 69
	Av. internode	..	..	2	7	6	5	17	5	3	1	1	..	3	..	1	2	1	..	1	..	..	..	..	1	..	..	..	56	2 29

three characters, culm length, rachis length, and rachis internode length, are shown in table 31, together with their means. The F_3 lines included in this table are arranged according to the order in which they were planted—38-3, 38-4, 38-5, and so on, representing successive rows of plantings. An inspection of the table shows that these three characters —length of culm, length of rachis, and average internode length—are more or less closely correlated. As a rule the lines with long culms produced lax plants and those with short culms yielded dense plants. It is seen from the curves in figure 84, prepared from the data in table 31, that

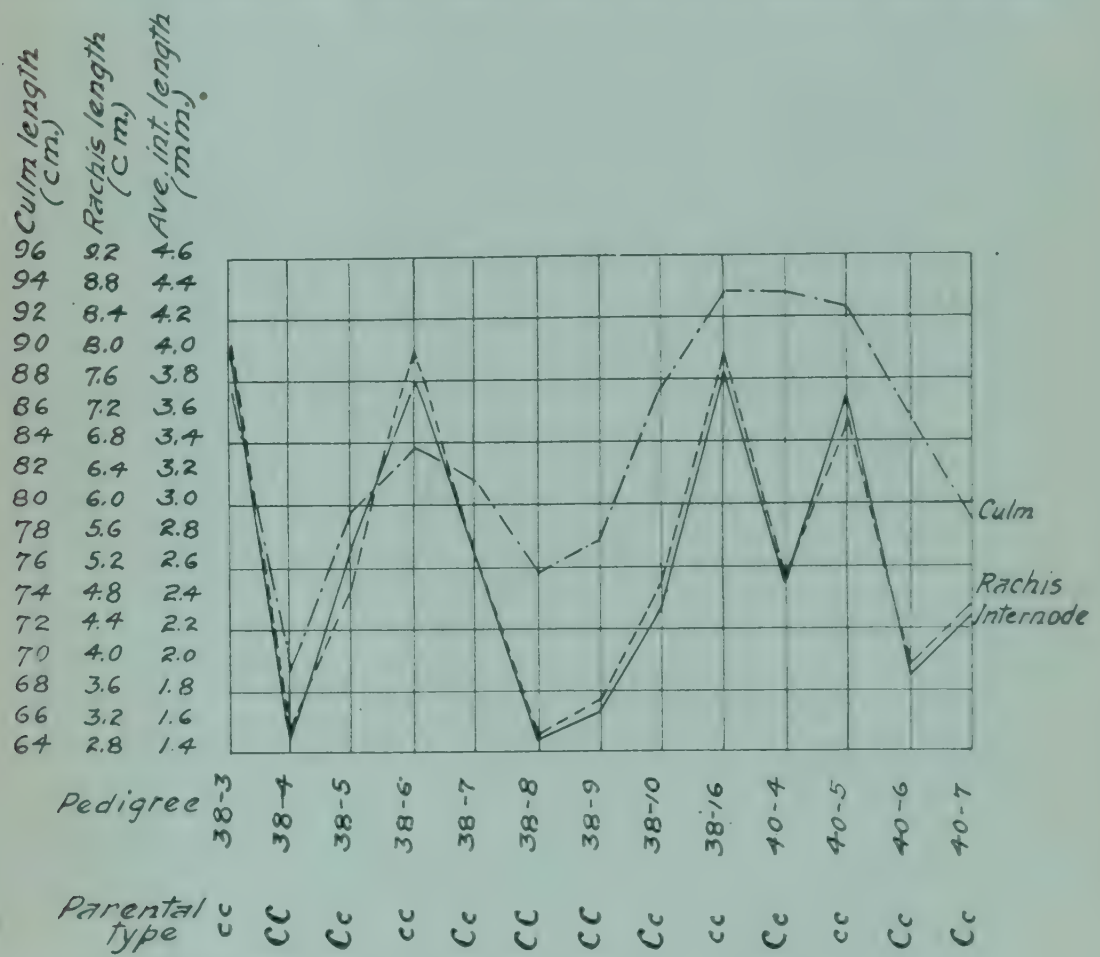

FIG. 84. AVERAGE CULM, RACHIS, AND INTERNODE LENGTH OF SOME F_3 FAMILIES OF SERIES 13214a

The curves show the relation of culm length to rachis and internode length. The order of the families corresponds to the order in which they were planted

when the mean of one of the characters decreases or increases, the others vary as a rule in the same direction.

There being no inherited variation in number of internodes (which averages about 20 to the spike) in the F_3 lines, the curves of rachis length and average internode length follow each other very closely. The curve of the culm length, although in a general way varying with density, shows certain irregularities, especially in the case of lines 38-6 and 40-4. The former is a homozygous lax type and the latter is heterozygous; yet the mean culm length of the former is considerably less than that of the latter, although theoretically it should have been greater. The possibility of the effect of environmental conditions being out of the question, it appears that there is a segregation of culm length independent of the dwarfing caused by the presence of the *C* factor. This statement is made as a suggestion only, since at the present time no definite explanation can be given.

A fact which seems rather interesting is that the *C* factor does not shorten the culm length in the same proportion as it shortens the rachis length. The averages of the rachis and culm lengths of the homozygous lax (*cc*) plants were about 7.7 centimeters and 89 centimeters, respectively. The presence of the double dose of the *C* factor (in 38-4, 38-8, and 38-9) shortened the rachis length to an average of 3.2 centimeters and the culm length to about 74 centimeters, a shortening of 58 and 17 per cent, respectively, from the general average. In other words, while the rachis length was shortened by the *C* factor by more than one-half, the culm length was shortened but one-sixth.

Studies of the characters of dense and lax segregates have led the author to believe that the *C* factor is a dwarfing factor, shortening, besides the culm length, the rachis length, and the rachis internode length, a number of other characters such as length of glumes, length of kernels, length of awns, and length of culm internodes. These two last-named characters have not been studied carefully by the author. Sapehin (1916) and his collaborators, who studied the correlation between density and culm internode length, claim that there is a significant positive correlation between these two characters. From the present studies it seems apparent that the shortening of the culm as a result of the pres-

ence of the factor for density, is due not to the reduction in number of culm internodes, but to the reduction in length of the culm internodes, the number of these internodes remaining more or less constant. In this respect the phenomenon of the shortening of the culm is similar to that of the shortening of the rachis. It has been demonstrated by various workers that in maize also dwarfing causes the shortening of the internodes of the stalk without necessarily affecting their number.

In a general statement such as is made here regarding the presence of a correlation between density of the head and shortness of the culm, it is not intended to convey the idea that dense plants or varieties are all to be short, and lax plants tall. The cardinal points brought out are (1) that when the factor of density or its absence has been introduced in a progeny through hybridization, provided there are no interfering factors, the dense plants will be more likely to have short culms than the laxer plants; and (2) that this shortening of the plant is caused, not by the reduction in number of culm internodes, but by the reduction in their length. It should be borne in mind, however, that these characters are affected by environment. From a genetic viewpoint the exhibition of a quantitative character in an individual plant is of little value especially if this is affected by environment. The comparative height of a plant is determined by the behavior of its progeny.

CORRELATION BETWEEN AVERAGE INTERNODE LENGTH AND LENGTH OF STERILE GLUMES

One of the proofs that the density factor is a dwarfing factor is found in the high degree of correlation existing between the average internode length and the length of the sterile glumes. The material for the study of this correlation consisted of the spelt plants of series 13255a-15, representing a cross between Dale Gloria and White Spelt. This F_3 line segregated into dense and lax *sativums* and spelts. In the data here only the spelts are represented. The spelts were selected primarily because the glumes could be readily removed from the spikelets, as they break off uniformly at the base of the glume at a definite region just below the heel. With *vulgare* forms the taking of measurements is somewhat more laborious. The measurements of the glumes recorded here rep-

resent the average of the length of opposing sterile glumes on the same spikelet at a distance from the base of the spike of about one-third the length of the rachis. This precaution was taken because the glumes shorten as they approach the distal or the basal part of the head.

The correlation between average internode length and glume length is represented in table 32. The correlation coefficient here is 0.838 ±

TABLE 32. CORRELATION BETWEEN DENSITY AND LENGTH OF STERILE GLUMES (Series 13255a-15, Dale Gloria x White Spelt; only the spelts measured)

Average internode length (in millimeters)	Length of glumes (in millimeters)								
	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5
1.5	1	1	1						
2.0		3							
2.5		3	6						
3.0		1	1	3	2				
3.5					1				
4.0					2				
4.5				1	2	1	1	2	
5.0						1		1	1
5.5							1	1	
6.0					1	1			1

r = 0.838±0.039

0.039, which shows significantly that in this particular cross the factor decreasing rachis internode length is the one causing the shortening of glumes. The relation of density to glume length may be readily seen on heads 6, 7, and 8 in Plate LXVII (upper), which show the grades of density and consequently of glume length.

CORRELATION BETWEEN AVERAGE INTERNODE LENGTH AND LENGTH OF KERNELS

The same degree of correlation exists between density and length of kernels as between density and glume length. The measurements of the length of the kernel as here recorded represent the average length of the first and second kernels developed on the basal florets. Of these two kernels the first was very often longer than the second. In cases in which either the first or the second basal floret had not produced seed, the third seed was not measured in its stead because the third seed is always likely

to be smaller. In such cases a different spikelet was chosen, the samples being taken always at a distance from the base of the head of about one-third the length of the rachis.

Correlating these two characters as shown in table 33, a correlation

TABLE 33. CORRELATION BETWEEN DENSITY AND LENGTH OF KERNELS
(Series 13255a-15, Dale Gloria x White Spelt; only the spelts measured)

Average internode length (in millimeters)	Length of kernels (in millimeters)											
	5.6	5.8	6.0	6.2	6.4	6.6	6.8	7.0	7.2	7.4	7.6	7.8
1.5		1			1		1					
2.0	1			1	1							
2.5	1			2	5	1						
3.0				3	1	1	2					
3.5						1						
4.0							2					
4.5								5		2		
5.0									1		1	1
5.5								1		1		
6.0						1	1		1			

$r = 0.747 \pm 0.024$

coefficient of 0.747 ± 0.024 is obtained. Compared in terms of the respective probable errors, this is as high as or slightly higher than the correlation between density and glume length.

The width of the kernels was not affected by the length of the kernels or by density. This density factor does not seem to produce diminutiveness but to shorten along one axis only. The width of the kernels, whether taken laterally or dorsi-ventrally, remaining practically the same, the shape of the kernels assumes a spheroid form among the dense segregates and a long spindle form among the lax plants.

Since density is correlated with length of glume and length of kernel, it is obvious that in this material there is also a direct correlation between length of glume and length of kernel.

RELATION OF DENSITY OF RACHIS TO DENSITY OF RACHILLA

A rachilla is the rachis of a spikelet, and branches out from the main rachis. A spikelet may have three or more rachilla internodes; the basal one is very short, but toward the terminal part of the spikelet the internodes elongate and then shorten again.

It is practically impossible to measure the average rachilla internode length. For comparative purposes, however, the relation of density to average rachilla internode length can be determined indirectly by noting the extent of the protrusion of the fertile glumes of the florets. The relative distance between the fertile glumes of the first and the third floret on different wheat heads indicates their relative rachilla internode length, as is illustrated in figure 85.

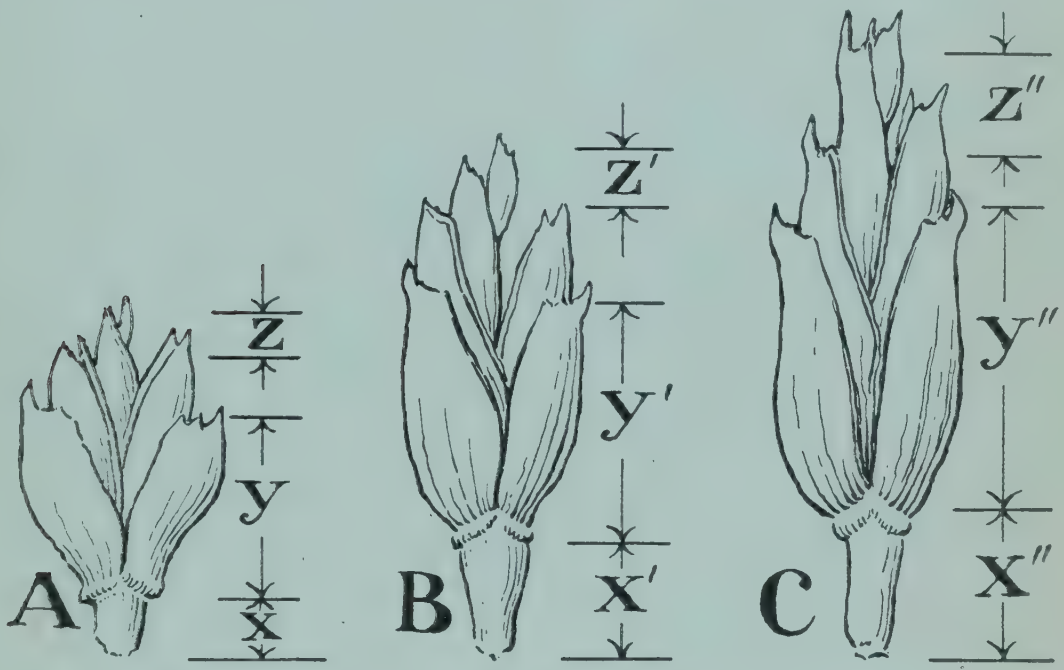

FIG. 85. SPIKELETS OF SPELTS OF VARYING DEGREES OF DENSITY, SHOWING RELATION OF INTERNODE LENGTH (x, x′, AND x″) TO LENGTH OF STERILE GLUMES (y, y′, AND y″) AND RELATIVE RACHILLA INTERNODE LENGTH AS DETERMINED BY DISTANCE BETWEEN THE TIPS OF THE FERTILE GLUMES OF THE FIRST AND THIRD FLORETS (z, z′, AND z″)

To bring out the correlation between rachis and rachilla internode length it is necessary to find a population comprising wheat plants of the same species which are segregating into dense and lax forms.

Dense and lax spelt plants of series 13255a-15 are reprersented, respectively, in *A* and *B* of figure 85. The illustration shows that the laxer was the form, the more did the florets protrude above the two sterile glumes. In figure 85, *C*, is represented the appearance of a synthetic spelt of un-

usual length derived from a *durum* x *vulgare* cross. It shows a further increase in rachis internode length, together with a relative increase in glume length.

These observations, which unfortunately cannot be presented in the usual form of a correlation table, indicate that *C*, the factor for compactness, shortens also the length of the rachillae or that of their internodes.

THE FACTOR FOR SPELTING ACTING AS A MODIFIER FOR THE DENSITY FACTOR

Density, like squareheadedness, is affected to a large extent by the presence of the spelt factor. In series 13255a, which represents a cross between White Spelt and Dale Gloria (Plate LXVII, upper, 4 to 12), there is but one spelt factor. Spelts and *sativums* segregate in this cross in the simple monohybrid ratio of 3 spelts of all grades (heads 6, 7, and 8) to 1 *sativum* (which includes *compactum* [heads 9 and 10], squareheads [head 11], and *vulgare* [head 12]). In a cross in which one of the parents is a spelt, the inheritance of density cannot be studied if all the plants are classified according to density alone, for, as will be seen, in the presence of the factor for spelting the factor for density does not produce compactness in the same degree as it does in the absence of the spelt factor. Therefore, in determining the mode of inheritance in such cases, it is necessary to take into consideration both the degree of spelting and the density, and in interpreting the data the density curves of the spelt and those of the *sativums* should be examined separately.

The difference in density of the spelt and the *sativum* form may be best illustrated by the density curves of the progeny of the two F_2 plants, one of which was homozygous dense and the other was homozygous lax, but both of which segregated into spelts and *sativums*. The relative density of spelts and *sativums* is shown in table 34. The plants of 13255a-26 are segregates from the Dale Gloria x White Spelt cross. They are all homozygous dense, but are derived from F_2 plants heterozygous for the spelting character. If *S* stands for the spelting factor and *C* for compactness, the F_3 progeny of line 13255a-28 consists of *SSCc*, *Sscc*, and *sscc* individuals, while 13255a-26 consists of *SSCC*,

TABLE 34. COMPARISON OF DENSITY OF SPELT AND SATIVUM SEGREGATES OF TWO F_3 PROGENIES, ONE HOMOZYGOUS DENSE BUT HETEROZYGOUS FOR SPELTING, THE OTHER HOMOZYGOUS LAX BUT HETEROZYGOUS FOR SPELTING
(Series 13255a, Dale Gloria x White Spelt)

Pedigree	Type	Average internode length (in millimeters)																			Number of plants	Difference between means
		1.3	1.5	1.7	1.9	2.1	2.3	2.5	2.7	2.9	3.1	3.3	3.5	3.7	3.9	4.1	4.3	4.5	4.7	4.9	Mean	
-26	Homozygous dense																					
	Spelts	....	1	8	6	3	1	3	2	..	..	..	..	..	..	..	..	..	..	..	2.00	24	
	Sativums	2	5	4	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.57	12	
																							0.43
-28	Homozygous lax																					
	Spelts	....	..	..	..	..	..	..	..	..	1	1	2	2	5	7	2	7	4	4	4.22	35	
	Sativums	....	..	..	..	..	..	3	7	6	1	..	..	..	..	..	..	..	..	..	2.76	17	
																							1.46

SsCC, and *ssCC* plants. The mean internode length of the lax spelts, as shown in table 34, was 4.22 millimeters; that of the *sativums* was 2.76 millimeters, showing a difference of 1.46. Of the plants homozygous for the density factor, the dense spelts had a mean internode length of 2.00 millimeters and the dense *sativums* one of 1.57, showing a difference of 0.43 millimeter.

From these results it is seen that, although the internode length of the spelts can be shortened by the introduction of the *C* factor, the presence of the *S* factor tends to interfere with the effect which a known *C* factor would otherwise produce.

The relation of the *S* factor to density is the same as the relation of this same factor to squareheadedness. It has already been shown that the presence of factors for squareheading have a very slight effect on the heads that carry the factor for spelting.

THE SYNTHETIC PRODUCTION OF TRITICUM COMPACTUM

Triticum compactum, as has already been shown, is but a form of *Tr. sativum*, which carries an additional factor or factors for compactness. The results of crosses between different species show that this same factor can be carried as well by any of the other species of Triticum. In fact, there will be found in commercial strains species that carry density factors, though not necessarily the same factor. Many forms of *durum*, and especially of *dicoccum*, carry a density factor. When these are crossed with a lax *vulgare* form, compact forms invariably appear in varying proportions, and, depending on the genotypic forms of the plant, some of these compact forms breed true while others segregate.

In order to produce compact forms, it is not necessary that one of the parents should be a dense form. If the plant is carrying an inhibiting factor besides the factor for density, it may appear lax although it has the potentiality of producing dense forms. Thus, Black Bearded Spelt, which has been used by the author, is perfectly lax, but when crossed with *vulgare* it produces lax spelts in the F_1, and in the F_2 an appreciable number of perfectly dense forms. The White Winter Spelt, on the other hand, produces no compact forms. The Black Bearded Spelt, then, carries a factor for compactness and also an inhibiting factor. Certain

forms of *turgidum, durum*, and even *polonicum* also have the ability to produce dense types in the F_2.

The writer has had no experience with *vulgare* crosses which have produced compact forms in the F_2; and unless the inhibiting factor is closely linked with the factors producing a certain specific form, it seems possible that certain *vulgare* forms will be met with which, although carrying the density factor, will be lax because of the presence of an inhibiting factor.

The mode of inheritance of density in some species crosses is very complex, because new specific forms arise in such crosses, each of which is affected in a peculiar way by the density factor. Besides factors for inhibition, many modifiers also may be involved. Often irregularities are produced by the failure of development or maturation of some forms which seem to carry combinations of growth factors that restrict growth or cause various anomalies. Before being able to analyze from a factorial point of view the inheritance of density in such crosses, it is necessary to know in what proportions the various specific forms segregate.

There are two cases which suggest that compact or semi-compact *vulgare* forms have been obtained through crossing two *vulgare* forms. De Vilmorin (1913) cites two instances in which lax forms produced dwarf forms. The dwarf plant, a photograph of which accompanies the text, appears to be a compact form much denser than the plant from which it mutated. It may also be possible that these cases were natural crosses with a *compactum* pollen, since segregation of other characters occurred also. Another case is that mentioned by Neethling (1918), in which tall *vulgare* forms crossed among themselves yielded dwarf forms. The latter behaved as recessives. The statement is made that the dwarf plants had short ears, but nothing is said about density. If these were *compactum* forms, the fact that these dwarf forms appeared in a proportion somewhat less than 25 per cent tends to lend support to the possibility that the parent which carried the density factor carried also a factor inhibiting the production of dense forms. Until more is learned about the behavior of the F_2 in the F_3, no definite explanation can be given to account for its mode of inheritance.

In Plate LXVII (lower) are shown a number of dense forms of different wheat species, most of these being synthetically produced in interspecific crosses. Some show both compactness and squareheadedness; others show one of these characters in the absence of the other. Körnicke (1885) has observed dense and squarehead varieties in other wheat species. He gives the following botanical varieties: *Triticum durum* Desf. var. *compactum* Sér., *Tr. polonicum* L. var. *compactum* Link., *Tr. polonicum* L. var. *quadratum* Sér., and *Tr. turgidum* L. var. *quadratum* Sér.

Density, or the excessive shortening of the rachis internodes, is not confined to the genus Triticum. Dense forms are common both in barley and in rye.

The question of the origin of *Tr. compactum* becomes simplified if it is recalled that this form may be produced when a *sativum* form is crossed with another wheat species, and also that natural crossing occurs not infrequently. Such being the case, one would expect *Tr. compactum* to be practically as old a form as any of the other species, and, so far as archaeological evidences go, cultivation of *Tr. compactum* has been traced as far back as the Stone Age. Buschan (1895) states that this compact form has been found in the remains of caves and lake dwellings and among other prehistoric relics in regions extending from Egypt to central Europe and to Sweden. According to Unger (1860), the culture of wheat has been traced back to the year 3623 B. C., and hence its origin must be older still.

If interspecific crosses between *vulgare* and other forms are able to produce compact forms, it seems that the first origin of *Tr. compactum* should have followed that of *Tr. vulgare*. Undoubtedly *Tr. compactum* has reappeared many times in the same manner, for the appearance of this form in interspecific crosses is rather common. *Tr. compactum* may be a mutational form of *vulgare*, although there is no dependable evidence regarding this possibility for *vulgare* wheats. There is a parallel example in the case of the rye known as "Heinrich-Roggen" (Hillmann, 1910: 579). This is a very compact form of rye which is said to have appeared in 1880 as a mutation on a single ear.

SUMMARY

The density studies reported herein were made primarily on the progeny of a number of crosses in which the dense parent was Dale Gloria (*Triticum compactum*), with an average internode length of about 1.41 millimeters.

Density was found to be dominant over laxness. The ratios obtained approached 3:1. The heterozygous forms were somewhat laxer than the homozygous dense forms, but by no means intermediate between the dense and the lax parents. The F_2 curves were bi-modal and discontinuous.

The F_3 plants showed various degrees of density within the dense and the lax classes. Proofs are given in the text showing that these variations are hereditary and are the result of the segregation of modifiers or of additional density factors capable of producing density only within short ranges.

Experimental evidence is cited suggesting that different density factors form allelomorphic series, and other evidence that they belong to multiple series.

Squareheadedness and density were found to represent two different characters. Hybrid progenies showed all types and grades of combinations between these two characters.

The process of squareheading was found to shorten the average internode length. The effect on density thus produced, however, is slight.

The phenotypic transmission of the squareheadedness of Dale Gloria is dependent on the type of the lax non-squarehead parent. In some crosses there was a large proportion of lax squarehead forms in the F_2, while in others there were none of these forms.

Although in F_2 progenies resulting from dense and lax crosses an almost perfect correlation exists between rachis length and density, these two characters are not necessarily correlated. Rachis length is the indirect product of average internode length and number of internodes. The correlation between density and rachis length becomes less and less as the difference between the number of internodes of the parental forms increases.

High degrees of correlation were found between average internode

length and length of culm, length of sterile glumes, and length of kernels, and average rachilla internode length. These, together with other observations, show that density and the shortening of these other length characters are the result of a single dwarfing factor.

Plants exhibiting the spelt character are not as much affected by the density factor as are those that show *sativum* characters.

Compact forms may be produced by crossing a lax *sativum* with lax forms of other species. Dense forms may also appear occasionally in crosses where neither parent is a *sativum*. Compactness is not a characteristic of *sativum* forms; other species also may exhibit this character.

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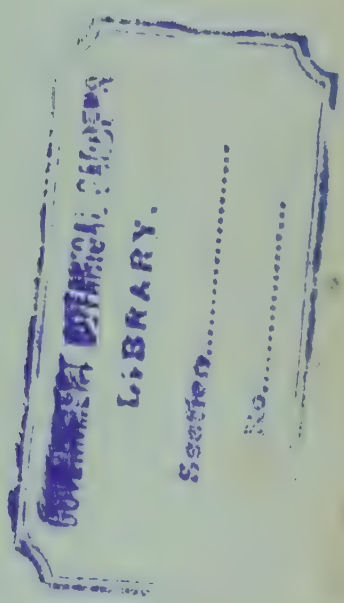
CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

INSECTS AND OTHER ANIMAL PESTS INJURIOUS TO FIELD BEANS IN NEW YORK

I. M. HAWLEY



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CONTENTS

PAGE

The seed-corn maggot (*Hylemyia cilicrura* Rond.) 949
Systematic position 950
Common names 950
History 950
Distribution 951
Food plants 951
Nature of injury to beans 952
Injury to the plumule 952
Injury to the cotyledons 955
Injury to the radicle 955
Loss caused 955
Description of stages 956
The egg 956
The larva 956
The adult 956
Life history and habits 958
The egg 958
Period of incubation 958
Place of oviposition 959
Number of eggs 960
Time of oviposition 960
The larva 961
Length of larval stage 961
Habits of the larva 961
The pupa 962
Time spent in puparium 962
Place of pupation 962
The adult 962
Emergence 962
Length of life 964
Habits 964
Hibernation 965
Seasonal history 966
Control 966
Artificial methods of control 966
Natural and cultural methods of control 970
Moisture and temperature as factors in the life of the seed-corn maggot 970
Relation of time of bean planting to time of oviposition 972
Relation of kind and condition of soil to maggot infestation 974
Influence of preceding crop and time of fitting a field, on maggot attack 974
Relation of depth of planting to injury by maggots 975
Summary of preventive measures 976
The imported field gray slug (*Agriolimax agrestis* L.) 977
Origin 977
History and distribution 977
Systematic position 978
General description of the slugs of the family Limacidae 978
Ancient superstitions concerning slugs 979
Peculiar habits of slugs 979
Economic importance 980
Nature of the injury to beans 980
Injury to plants other than beans 982
Hosts and possible food supplies 982
Description of stages 983
The egg 983
The young slug 983
The full-grown slug 983

PAGE
The imported field gray slug (*Agriolimax agrestis* L.) (*continued*)
Life history and habits ... 984
The egg ... 984
The young slug ... 985
The full-grown slug ... 986
Method of feeding ... 987
Mating and oviposition ... 987
Time required to reach maturity ... 987
Nature of outbreaks ... 988
Relation of *Agriolimax agrestis* to moisture ... 989
Relation of *Agriolimax agrestis* to extremes of temperature ... 989
Seasonal history ... 990
Predatory and parasitic enemies ... 990
Control ... 990
Experimental work ... 991
Summary of control suggestions ... 997
How to distinguish the various species of slugs found in bean fields ... 998
Agriolimax campestris Binney ... 998
The spotted garden slug, *Limax maximus* L. ... 999
Arion circumscriptus Johnson ... 999
The pale-striped flea beetle (*Systena taeniata* Say) ... 1000
Description of stages ... 1001
The egg ... 1001
The larva ... 1001
The pupa ... 1001
The adult ... 1002
Life history and habits ... 1002
The egg ... 1002
The larva ... 1002
The pupa ... 1003
The adult ... 1003
Seasonal history ... 1004
Control ... 1004
The red-headed flea beetle (*Systena frontalis* Fab.) ... 1005
Description of stages ... 1006
The egg ... 1006
The larva ... 1007
The adult ... 1007
Life history and habits ... 1007
The egg ... 1007
The larva and the pupa ... 1008
The adult ... 1008
Seasonal history ... 1008
Control ... 1009
The green clover worm (*Plathypena scabra* Fab.) ... 1011
The bean weevil (*Acanthoscelides* [*Bruchus*] *obtectus* Say) ... 1014
The blue-banded millepede (*Julus caeruleocinctus* Wood) ... 1015
The solanum root louse (*Trifidaphis radicicola* Essig) ... 1017
The wheat wireworm (*Agriotes mancus* Say) ... 1018
The red spider (*Tetranychus telarius* L.) ... 1018
White grubs, or May beetles (*Phyllophaga* sp.) ... 1019
The rose chafer (*Macrodactylus subspinosus* Fab.) ... 1019
The southern corn rootworm (*Diabrotica duodecimpunctata* Fab.) ... 1020
The bean leaf beetle (*Cerotoma trifurcata* Forster) ... 1020
The apple leaf hopper (*Empoasca mali* LeB.) ... 1021
Grasshoppers (*Melanoplus atlantis* Riley, *M. femur-rubrum* DeGeer, and *M. bivittatus* Say ... 1021
Injuries to beans in the pod, caused by hemipterous insects (*Adelphocorus rapidus* Say, *Euschistus variolarius* Palisot de Beauvois, *Lygus pratensis* L. ... 1021
The rôle of insects in the transmission of bean diseases ... 1023
Bibliography and literature cited ... 1025

INSECTS AND OTHER ANIMAL PESTS INJURIOUS TO FIELD BEANS IN NEW YORK

INSECTS AND OTHER ANIMAL PESTS INJURIOUS TO FIELD BEANS IN NEW YORK

I. M. Hawley

In June, 1917, a laboratory was established at Perry, in the bean-growing section of western New York, for an investigation of the diseases and the insects that had been causing much injury to field beans. In this work the Departments of Entomology, Plant Breeding, and Plant Pathology at Cornell University were each represented by one member. This investigation has been carried on for four years, and the results, on the whole, have been satisfactory. The entomological work, however, has been hindered by one unavoidable circumstance: in some summers the insect pests under investigation were very scarce, and field experiments for their control were thus impossible. As a result, the recommendations in some cases are based on fewer data than the writer had wished.

The more important part of this investigation is the part concerning the seed-corn maggot (*Hylemyia cilicrura* Rond.). The field gray slug (*Agriolimax agrestis* L.), a mollusk of the family Limacidae, also has been studied in detail, and some attention has been given to the green clover worm (*Plathypena scabra* Fab.), the red-headed flea beetle (*Systena frontalis* Fab.), the pale-striped flea beetle (*Systena taeniata* Say), the blue-banded millepede, or thousand-legged worm (*Julus caeruleocinctus* Wood), and the bean weevil (*Acanthoscelides obtectus* Say). Observations were made also on the habits of some insects of lesser importance, in particular those that produce the pitting of the bean known as *dimpling*.

THE SEED-CORN MAGGOT
(*Hylemyia cilicrura* Rond.)

It is difficult to obtain exact data concerning *Hylemyia cilicrura*,[1] for it is an erratic insect that may occur in a field in great numbers in one season, and not reappear in, or even near, that field the following year. The flies usually disappear in late summer and the hosts of the larvae during that part of the year are not definitely known. Reared flies apparently do not mate in captivity. Infestations of the insect in cultivated crops are not usually found until considerable damage has been caused. By that time the maggots are full-grown and it is too late for control experiments with that brood. The writer realizes the many gaps in the present work, but, as the insect is scarce at the present time, it seems desirable to record the results thus far obtained.

[1] This species is more commonly known in American literature on economic entomology as *Phorbia fusciceps* Zett.

SYSTEMATIC POSITION

The parent insect of the seed-corn maggot (*Hylemyia cilicrura*, Plate LXIX, 1) is a fly of the order Diptera and the family Anthomyiidae. The insect was first described by Rondani (1866)[2] as *Chortophila cilicrura*. Until recently, however, *cilicrura* has been considered synonymous with *fusciceps* of Zetterstedt (1845), and, since Zetterstedt's description precedes that of Rondani, *fusciceps* has been accepted as the specific name of the insect. Stein (1916) finds that *fusciceps* is a distinct species and not the *cilicrura* of Rondani. Malloch (1920) accepts the separation of the two species made by Stein. The species *fusciceps* of Zetterstedt occurs in Lapland and other parts of northern Europe, and recently Malloch (1920) has recorded it from North America. The species *cilicrura*, in addition to a wide European distribution, is present in most parts of North America, and is the pest known as the seed-corn maggot. The *fusciceps* described by Slingerland (1894) is not the *fusciceps* of Zetterstedt but is *cilicrura* Rond.

Stein (1916) places *cilicrura* in the genus Chortophila, but Malloch (1920) unites the genera Chortophila, Phorbia, and Hylemyia in the strict sense, in the genus Hylemyia. If we follow this latest paper on the subject, the seed-corn maggot must be called *Hylemyia cilicrura* Rond.

In the recent European writings of Reh (1913) and Oberstein (1916), the specific name *Chortophila cilicrura* is applied to this insect; but in older works, such as that of Ritzema Bos (1890), mention is often made of *Anthomyia platura*. The species *platura* is a composite of *cilicrura* and *trichodactyla*, and often it is impossible to determine definitely which species was blamable for the work these authors have described.

COMMON NAMES

The common names given to *Hylemyia cilicrura* include the following: deceiving wheat fly, locust-egg anthomyian, Anthomyia egg parasite, seed-corn maggot, corn Anthomyia, seed-corn flower-fly, bean maggot, bean fly, fringed anthomyian. Of these, the name *seed-corn maggot* is the best known and is the one retained in this paper.

HISTORY

Hylemyia cilicrura is probably of European origin. In North America the first record was that of Fitch (1856), who found the fly on wheat heads and described it under the name *Hylemyia deceptiva*. Riley (1869) discovered the larva attacking corn in New Jersey and named the fly *Anthomyia Zeae*, but nine years later (Riley, 1878) he called it *Anthomyia angustifrons* Meigen when he found the maggots feeding on locust eggs in Kansas and other western States. It was reported that ten per cent or more of

[2] Dates in parenthesis refer to *Bibliography and Literature Cited*, pages 1025 to 1037.

these locust eggs were destroyed in this way. Later, Jack (1886) found the maggots destroying field beans in Canada. At intervals since that time the pest has suddenly appeared, destroying bean seedlings and injuring many other crops both in the United States and in Canada.

During the last few years *H. cilicrura* has once more become active in the New York bean fields, after a period of scarcity covering many years. Since 1914 moist weather conditions have tended to augment the normal number of flies. The injuries caused by the maggots of this species reached a maximum in 1917, but since that time there has been a gradual decrease in the amount of damage, and in 1919 and 1920 the loss due to the insect was hardly noticeable.

DISTRIBUTION

The seed-corn maggot has been found in many parts of the United States and Canada. It has been reported from nearly every State, from Maine to Florida and westward to the Pacific. In Europe, reports of its presence in Austria, Germany, Italy, England, and France may be found. It has been reported also from Hawaii.

Chittenden (1916) states that the species *cilicrura* causes much of the loss in the States south of New Jersey which is credited to the cabbage maggot, *Hylemyia* (*Phorbia*) *brassicae* Bousché, and to the onion maggot, *Hylemyia antiqua* Meigen (*Phorbia ceparum* Meade). Chittenden believes also (1909) that some of the work on the Pacific Coast attributed to *Hylemyia planipalpis* Stein may be due to *H. cilicrura*.

FOOD PLANTS

Hylemyia cilicrura has a wide range of food plants, according to Chittenden (1902) and other writers. Among the commoner of these may be mentioned beans, peas, lettuce, corn, cabbage, cauliflower, beets, turnips, radishes, seed potatoes, sweet potatoes, domestic garlic, crimson clover, onions, and hedge mustard. Whelan (1916) reports the maggot as breeding in fresh manure, in clover and alfalfa sod, and in rotting clover stems. Tucker (1917) reports *cilicrura* injury on tomatoes and cauliflower, and says that the larvae were found developing in decomposed cotton seed. Garman (1904) found the insect in young hemp plants. Pettit (1910) mentions pumpkin, cotton, orange, artichoke, and strawberry as hosts. Parks[3] bred *cilicrura* from maggots in the "bulbs" of wheat. Howard (1900) states that the fly has been bred from human excrement. Riley (1878) found the maggots feeding on locust eggs.

The attraction of the insect for decaying matter has been recognized by many writers. Chittenden (1902) cites, as an example of this, the finding of the larvae in tineid galls on poplar trees. Quaintance and Jenne (1912) found the flies appearing in cages where decaying plums

[3] As stated in a general discussion reported in the *Journal of Economic Entomology*, vol. 9, p. 133, 1916.

were used in rearing the plum curculio. Johannsen (1911) thinks the species is attracted by decaying matter in the soil. Berger (1908) found the insect working in cut surfaces of seed potatoes that showed decay. Schoene (1916) has often bred the insect on cabbage, and believes the species is attracted to that plant by decomposition in parts of it. Blackman and Stage (1918) bred the species on a decaying root of larch.

The insect has been reported also in Europe. It was found on sea kale in England, and Ritzema Bos (1890) reported finding the species *platura* (which, as already noted, is a composite of *cilicrura* and *trichodactyla*) on human excrement, on asparagus, on leek (*Allium porrum*), and on shallot (*A. ascalonicum*). More recently this species has been discussed, under the name *Chortophila cilicrura*, as a pest of rye and corn in Silesia (Oberstein, 1916). Kornauth (1916) reports *trichodactyla* as injurious to beans in Moravia.

Under field conditions in western New York during the progress of the present study, larvae of *Hylemyia cilicrura* have been found in beans, peas, corn, seed potatoes, and alfalfa roots. Baits of decaying materials were placed near the laboratory, and later examination showed the following to contain maggots: cabbage, bean pods, bean vines, grass stems, clover roots, and clover stems. Two larvae have been found in mustard growing near a bean field, and two flies were bred from larvae taken in late summer in the roots of quack grass (*Agropyron repens*). The species has been reared also from pupae found in a pile of rich soil that had been taken from beneath decaying stumps. The writer has never bred the fly from manure.

From these data it may be seen that the list of known hosts is both large and varied, including not only healthy and decaying vegetable tissue, but also animal tissue. It is probable that this list is far from complete.

The first flies taken each spring have been found by sweeping old wheat fields, and the writer believes that wheat, oats, and possibly other grains, may constitute important late-season hosts; but as yet sufficient data are not available for proof of this. Mature females of the second brood, taken in July, were numerous near sod and quack grass, and these also may be common winter hosts of the insects.

NATURE OF INJURY TO BEANS

The larvae of the seed-corn maggot may feed on three parts of a bean seedling—the plumule, the cotyledons, and the radicle. The injury to each part of the plant is here discussed separately.

Injury to the plumule

When the small larva locates a source of food in a sprouting bean, it usually crawls between the cotyledons, or seed leaves, and feeds on the two leaflets of the plumule and on the small bud of the growing tip between

them (Plate LXIX, 4, and fig. 86, A). This vegetative part of the plant may be entirely eaten away so that when the seedling comes above ground

FIG. 86. INJURY BY HYLEMYIA CILICRURA

A, Types of injury in bean seedlings. B, Injured bean plants known as *snakeheads*, showing the result of feeding by the seed-corn maggot

only the cotyledons remain. This stunted form of plant is known to bean growers as a *snakehead*, or *baldhead* (fig. 86, B). Usually a snakehead shrivels up and dies, but occasionally one succeeds in producing accessory

buds and in developing leaves and a few flowers (fig. 87, A). At harvest time a plant of this type is found to bear few if any pods and is still a dwarf plant (fig. 87, B). The formation of snakeheads is the severest form

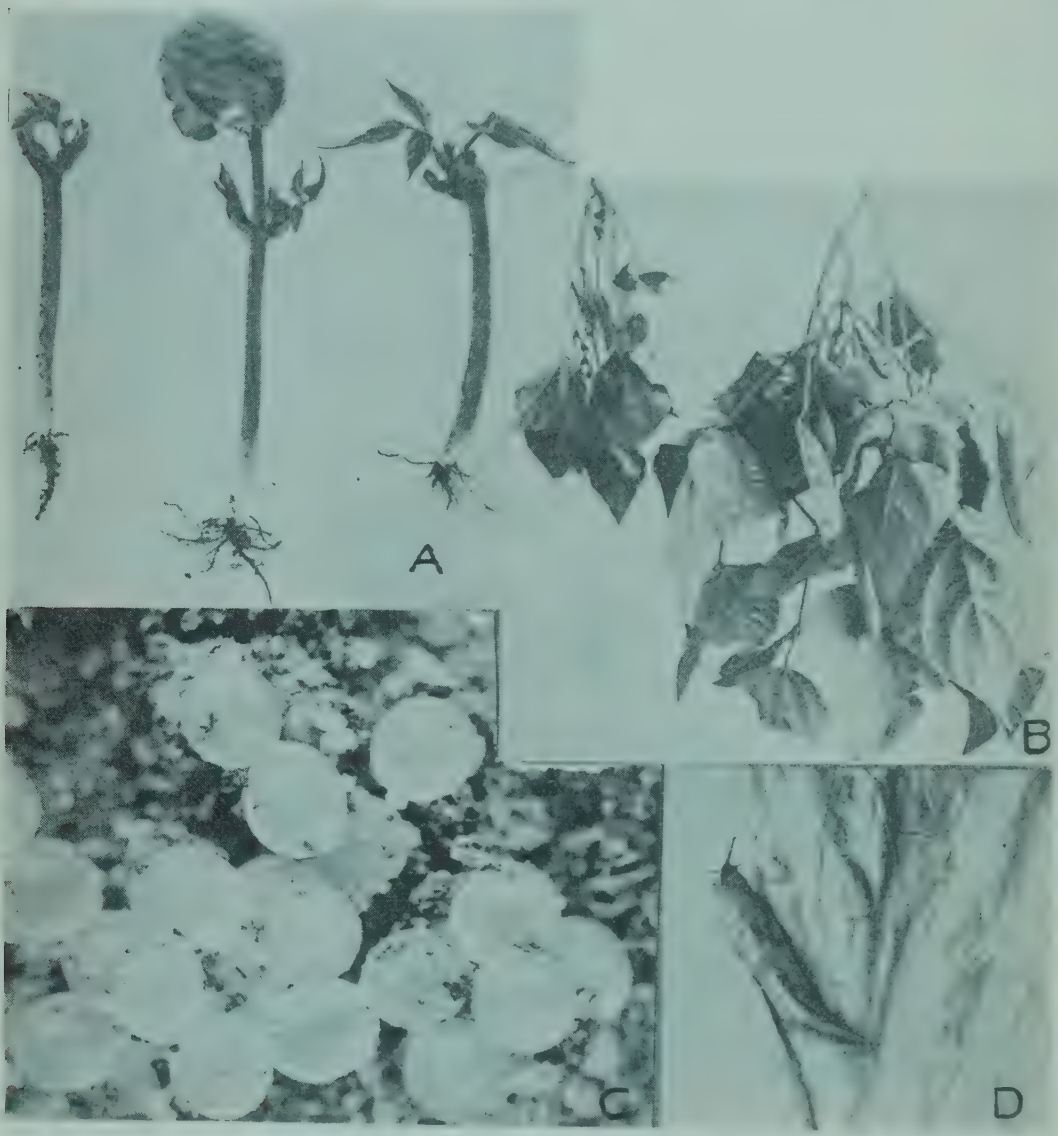

FIG. 87. RESULT OF WORK OF HYLEMYIA CILICRURA, AND EGGS AND ADULT OF AGRIOLIMAX AGRESTIS

A, Snakeheads putting out a new growth of small leaves. B, Two bean plants in late summer: the one on the left came from a snakehead, while the one on the right is a normal plant. C, Eggs deposited in the soil by *Agriolimax agrestis*, × 5. D, The field gray slug on a cabbage leaf, slightly reduced.

of injury to the bean caused by the seed-corn maggot, and in some fields the writer has found 75 per cent of the plants to be thus deformed.

If the maggot feeds on the leaf tissue of the plumule but does not destroy the growing tip, a thrifty plant may still result. The first two leaves may be misshapen and ragged, but new leaves are soon produced to take their places.

Injury to the cotyledons

Often a larva does not injure the cotyledons until it has fed on the plumule. Its entrance into a cotyledon is thru a hole made in the side, and the maggot usually hollows out the fleshy interior until little more than a shell remains. The maggots are often carried above the ground concealed in the cotyledons, and a single plant may have eight or even more hidden in these two seed-leaves. Damage to the cotyledons alone is not a serious handicap, as these are of little use to the plant after the true leaves have been formed.

Injury to the radicle

When a seed germinates so quickly that the cotyledons are pushed above the ground before any maggots locate the plant, the radicle may be attacked. The larva makes a small hole for its entrance and then mines upward thru the fleshy tissue of the stem. This injury is not serious, as the course of the maggot is thru the pith and it seldom disturbs the vascular tissue. In 1917 the writer observed a field near Batavia in which the beans were planted very deep. Soon after planting, a period of dry weather baked the top soil solid. The beans grew until they reached this upper impenetrable surface layer, and then they were bent over. Many maggots were found in the stem of each plant.

LOSS CAUSED

The year 1917 was a serious one for New York bean growers, because of the continued rains and the prevalence of maggots during the planting time, in June. In five townships of Genesee County the loss of seed attributed to *Hylemyia cilicrura* was estimated at $15,000. In Erie County the loss on 10,478 acres was said to be 40 per cent. In Monroe County from 50 to 75 per cent of the beans on 16,000 acres were destroyed, while in Orleans County one-fourth of $96,000 worth of seed was wasted. Many growers had to plant their beans two or three times, and one grower, who reseeded twice before getting a stand, estimated his loss for seed at $300. Similar injuries to bean crops were reported from New Jersey, Pennsylvania, Michigan, and Canada. At intervals in the past this insect has appeared thus suddenly and unexpectedly, has seriously damaged beans, corn, and other crops for a few subsequent years, and has then gradually disappeared for a time.

DESCRIPTION OF STAGES

The egg

The chorion, or outer covering, of the egg (figs. 88 and 89, C) is white, glistening, and marked with longitudinal furrows. Similar cross-furrows connect the longitudinal ones, cutting off irregular areas about twice as long as their width. One end of the egg is rounded and the other is rather bluntly flattened. Two prominent ridges, starting at either end of the flattened part, meet at a point about one-fourth the length of the egg. When the larva emerges, the chorion splits near these ridges. The length of the egg is about 1 millimeter (1/25 inch).

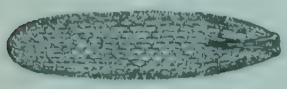

FIG. 88. EGG OF SEED-CORN MAGGOT, × 30

The larva

The full-grown larva (Plate LXIX, 2, and fig. 89, D) is white, and is largest at the caudal end, tapering anteriorly. In the early stages it is slender and almost conical, but as it nears the time for pupation it becomes shorter and almost elliptical in form. The first segment bears a pair of black, hooked jaws which may be extended and retracted. The anterior spiracular process is heavily chitinized and bears six or seven lobes. The posterior spiracles are small and consist of three slitlike openings with toothed edges. These spiracles, which are the external openings of tracheae running lengthwise thru the body, may be found on the flattened caudal end of the larva. This flattened, almost truncate, segment bears seven pairs of fleshy tubercles. The length of the larva is from 6 to 7 millimeters ($\frac{1}{4}$ inch).

The puparium.—The puparium (figs. 89, A, and 90) is brown in color and elongate-oval in outline. The puparium is the cast skin of the last molt of the larva, and so shows many larval characters. The anterior spiracles are present on the anterior part of the puparium and still show six or seven lobes. The fleshy tubercles on the caudal end of the body also remain but are less prominent. The length of the puparium is about 4 to 5 millimeters ($\frac{1}{6}$ to $\frac{1}{5}$ inch).

The adult

The male (Plate LXIX, 1, and fig. 89, B).—The body color of the adult male is greenish gray, with the legs darker and the antennae black. The entire body bears many black bristles. Faint dark lines run lengthwise on the dorsum of some specimens, and a prominent black line runs along the middle of the dorsal side of the abdomen. The main distinguishing character of the species is a row of regularly arranged bristles on the tibia of the hind leg (Plate LXIX, 3). This separates the species *ciliciura*

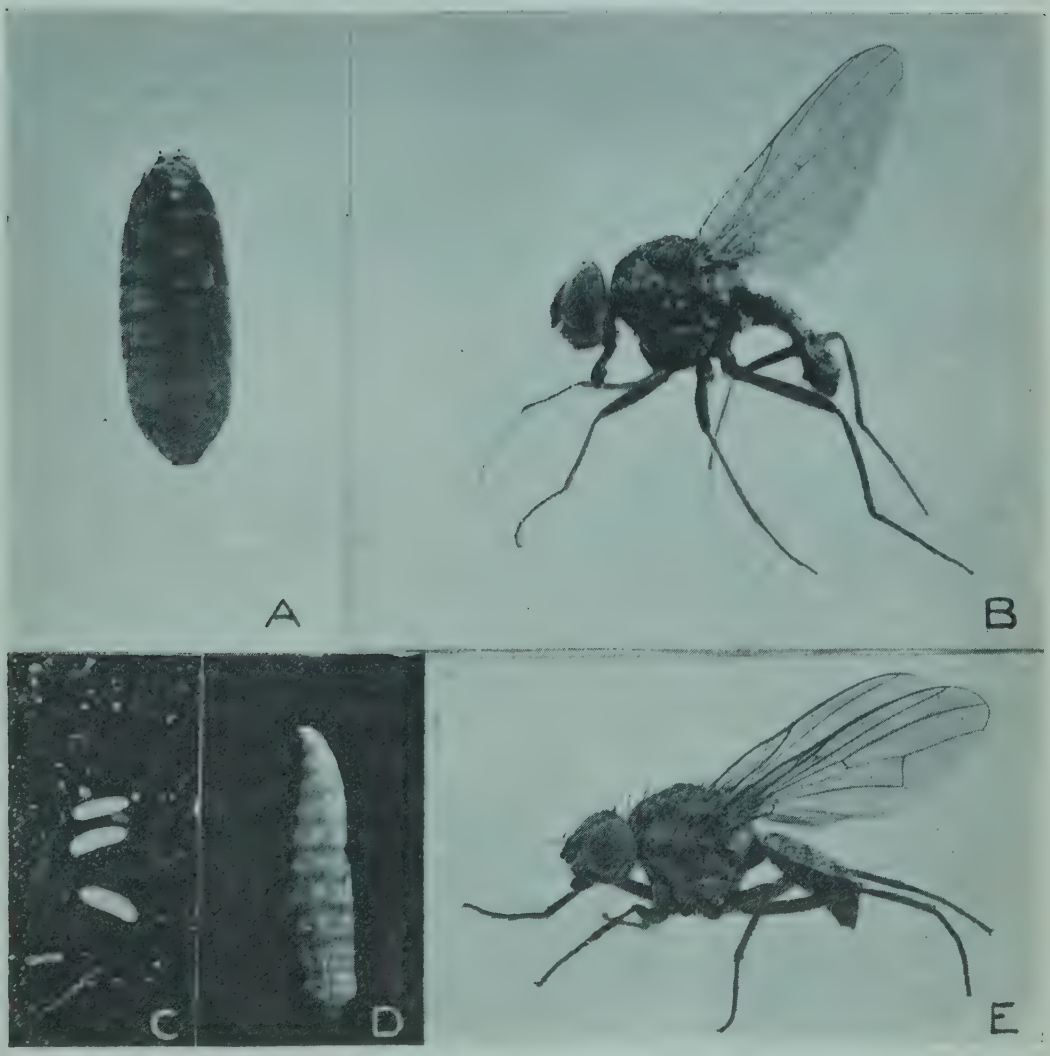

FIG. 89. THE SEED-CORN MAGGOT, HYLEMYIA CILICRURA

A, Puparium, × 8. B, Parent fly, male, × 10. C, Eggs, on dirt, × 6. D, Larva, × 5. E, Parent fly, female, × 10

from *brassicae* and *antiqua* (*ceparum*), with which it is often found associated in the field. In *brassicae* there is a tuft of fine setae at the base of the femur, which is lacking in *cilicrura*. In *trichodactyla* the middle metatarsus bears long hairs on the upper side, which are lacking in *cilicrura*. The length of the adult male of *cilicrura* is about 5 millimeters ($\frac{1}{5}$ inch).

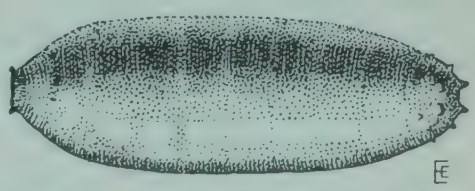

FIG. 90. PUPARIUM OF SEED-CORN MAGGOT, × $5\frac{1}{3}$

The female (fig. 89, E).— The female of *cilicrura* is similar to the male, but

the abdomen is pointed instead of rounded and the bristles on the body are fewer and shorter. The female lacks the prominent fringe of hairs found on the tibia of the male, and is harder to distinguish from related species. In *brassicae* the pre-alar bristle is as strong and as long as the first dorso-central one, while in *cilicrura* and *antiqua* it is only about half as long. In *antiqua* there are two nearly equal setae on the anterior (outer) side of the middle tibia, while in *cilicrura* there is usually but one. The species *antiqua* is ordinarily larger than *cilicrura*. The length of the female of *cilicrura* is 5 millimeters ($\frac{1}{5}$ inch).

LIFE HISTORY AND HABITS

The egg

There is little in the literature regarding the egg-laying of *Hylemyia cilicrura*. Whelan (1916) reports that the fly usually places its eggs either on the stems of plants just as they come thru the soil, or on decaying vegetable matter. Howitt (1911) states that the eggs are deposited on decaying matter in the soil. Lugger (1896) was able to bring about the deposition of eggs by flies in captivity, but he believed the eggs to be sterile for he failed in his attempts to rear flies from them. Chittenden (1909) mentions an instance in which decomposing crimson clover that had been plowed under attracted flies as a place for oviposition.

Period of incubation

In July, 1917, at Perry, New York, the length of the egg stage under very moist conditions was between 24 and 48 hours. Very few eggs were found and the exact time of oviposition was in doubt.

In 1918 eleven first-brood eggs under observation hatched in an average of 66 hours, as shown in table 1. There was a wide variation, from 41 to 91 hours, and many eggs, the exact hatching time of which could not be noted, hatched within these limits. Eggs were kept in petri dishes on moist blotting-paper or damp earth.

TABLE 1. LENGTH OF THE EGG STAGE IN 1918

Number of eggs	Time of deposition	Time of hatching	Length of stage (hours)
3	May 23, 3 p. m.	May 27, 9.30, 10, 10, a. m.	90.5, 91, 91
4	May 25, 4 p. m.	May 27, 9, 10, 10, 11.30, a. m.	41, 42, 42, 43.5
4	May 25, 3 p. m.	May 28, 9.30, 10, 10.30, 10.30, a. m.	70.5, 71, 71.5, 71.5

Average, 66 hours.

In 1919 notes were taken on the period of incubation of 28 eggs on moist earth. The average for these was 2.8 days, with a range from one to five days. Four eggs kept on dry blotting-paper in a petri dish required between three and four days. One egg, deposited on June 4, did not hatch until June 17, but this is the only instance of so long a period of incubation.

Place of oviposition

The insect is strongly attracted to moist and decaying material as a place for oviposition, but under some conditions the flies will place their eggs on dry material, as the following experiment shows. On June 4, 1919, many flies, taken by sweeping, were placed in a cage with a flower-pot containing dry bean stems and dry soil. This pot was kept dry until the flies died, after which it was moistened in order to see whether a new lot of flies would develop. On July 3 one fly was found in the cage, and on July 8 two more were found. In another cage the same conditions prevailed except that the jar was moist during the entire experiment. Four flies were found in this cage on July 3, and eight more on July 8.

In the field, eggs have been found around decaying bean pods and vines and around rotting cabbage. The writer has spent a great deal of time in looking for eggs on freshly plowed ground where mature flies were seen in large numbers, but has succeeded in finding only a few in such locations. Two eggs were found on newly turned soil and one was discovered in a crevice in a recently disked field. Egg-laying was induced by throwing water on the parched and cracking ground near the laboratory at a time when the flies were numerous. Eight eggs were found on top of the ground in one of these spots within two hours after it was thus moistened, and, in all, about one hundred eggs were obtained in this way.

Whelan (1916) says that the maggots of *H. cilicrura* are sometimes found in fresh manure. The writer, however, has not seen the larvae in manure, nor has he been able to bring about oviposition on manure. On June 5, 1919, flower-pots containing fresh cow, horse, hog, and hen manure were placed in a cage containing many adults of *cilicrura* that had been taken in the field. When these pots were examined later, no eggs could be found, and no flies ever emerged in the cage. On June 3, 1919, flies were placed in a large cage containing one flower-pot of manure of different kinds and another filled with decaying bean vines and grass sod. After the flies were all dead, the pot of manure was moved to another cage. No flies emerged from this pot. In the cage containing the pot with the decayed beans and grass sod, thirteen flies emerged. This apparently shows the insects' preference for decaying beans and clover rather than for animal manure, as a place for oviposition. Many times fresh manure found in fields where the flies were abundant has been placed in cages, but no flies have ever emerged. Furthermore, the flies have not been found in abnormal numbers around either manure piles or fresh manure dropped along the road.

Is it possible that manure has an attraction for the maggots developing from eggs deposited in the soil, which leads them to use it as a secondary host?

In cages, eggs of the first brood have been found singly as a rule, tho they have been found occasionally in groups of from two to five, in some cases side by side and in other cases piled on one another irregularly. When first-brood flies taken in the field were placed in cages, eggs were deposited on decaying mustard stems, on stems and roots of grass, on old bean pods and vines, and on cabbage stumps. Some eggs were found a so on the surface of the ground, and some in the top inch of dirt. A few were attached to the side of the flower-pot, both above and below the soil line. Eggs of the second brood were deposited by flies in captivity on top of the soil and in the dirt itself.

Number of eggs

The writer has not been able to bring about oviposition by flies reared in captivity, and accordingly he could not determine the exact number of eggs deposited by a single female. The following may be mentioned as typical examples of many dissected specimens. On May 27, 1918, 87 eggs, of which 25 were almost fully developed, were found in a dissected fly. On May 15, 1919, two flies were found with nearly mature eggs, one containing 30 and the other 48. In 1920 two flies were found containing 83 and 64 eggs, respectively, on May 7; and on May 19, five flies contained, respectively, 56, 25, 37, 85, and 72 eggs. It is believed that all the eggs in an insect mature at about the same time and that oviposition is completed within a few days. From these data it seems possible that a female may deposit 80 or more eggs, but the number may often be much smaller.

Time of oviposition

Since it is from the eggs of the first brood of flies that the maggots so injurious to growing crops are produced, special study has been given to this generation. Very little is known of conditions in 1917, as life-history studies did not begin until June 22. In 1918 adults were found containing well-developed eggs on May 9, and, tho some eggs were no doubt deposited by May 15, most of the eggs of the first brood were deposited between May 23 and June 1. Eggs of the second brood were deposited during the first half of July.

In 1919 eggs of the first generation were mostly deposited from May 20 to June 15, with the maximum deposition occurring about June 4. Second-brood flies were ready to oviposit between June 25 and July 4. Since a few flies were captured on September 13 and 15 whose abdomens contained immature eggs, it seems possible that a few eggs may have been deposited as late as October. However, these flies may hibernate, which would explain why a few flies with well-developed eggs are found in early May, several weeks ahead of most of the first brood.

The season of 1920 varied little from the two preceding years. The first flies were found on May 7, some containing eggs that were partly developed. Most of the eggs of the first brood were deposited during the first week of June. Eggs of second-brood flies were deposited early in July. The relationship between the time of oviposition and the dates of bean planting is discussed later (page 972).

The larva

Length of larval stage

The average length of the larval stage for eight specimens of *Hylemyia cilicrura*, which had been bred in vials in a field cage at the Perry laboratory in 1917, was 10.4 days, with a variation from 8 to 12 days. The data are given in table 2:

TABLE 2. BREEDING DATA FOR EIGHT FLIES REARED IN 1917

Date of hatching	Length of larval stage (days)	Date of beginning of pupal stage	Length of pupal stage (days)	Date of emergence of adult	Time from egg to adult (days)
July 17	12	July 29	20	August 18	32
July 17	11	July 28	14	August 11	25
July 18	12	July 30	11	August 10	23
July 25	8	August 2	10	August 12	17
July 25	10	August 4	12	August 16	22
July 26	9	August 4	12	August 16	21
July 26	9	August 4	16	August 20	25
July 26	12	August 6	15	August 21	27
Average	10.4	.....	13.7	.....	24

In June, 1919, the average larval period in the case of twenty-one first-brood maggots bred in the laboratory at Perry, was 9.4 days, with a range from 7 to 12 days. Specimens bred in the field cages required about two days more.

Habits of the larva

The larvae of *Hylemyia cilicrura* are instinctively internal feeders. When they hatch, the small larvae crawl thru the crevices of the soil in search of food. In this search they show a preference for material that is beginning to rot, and they are always most numerous in decaying beans. Seventeen maggots were once found in a slightly decomposed bean, and seven to ten is not an uncommon range. They may be found in sound

beans also, tho a sound seed rarely contains more than two or three. Beans that are entirely decomposed have no attraction for the insect.

In order to test the ability of a maggot to find its bean host, ten newly hatched larvae were placed on top of the soil in large vials, in July, 1917, and an unsoaked bean seed was placed at the bottom of each vial. Eight of the ten maggots found the bean and were reared to adults.

The pupa

Time spent in puparium

In the summer of 1917, the length of the pupal stage of eight specimens was found to be 13.7 days, as shown in table 2. The average length of the pupal stage of seventeen additional specimens, carried thru in the outdoor cage in July, was 12.8 days, the time varying from 10 to 14 days. In June, 1919, the average time required for nineteen pupae was 10.2 days, with a range from 8 to 14 days. The time required in a field cage, from the hatching of the egg until the emergence of the adult fly, was found to be 22.7 days for forty-five specimens, with a range from 16 to 27 days. Allowing 10 days for the larval stage, this would make the average pupal period 12.7 days. Cages have been examined for puparia tending to show a lengthened pupal period, but cases of retardation, such as those noted by Schoene for the closely related cabbage maggot (*Hylemyia* [*Phorbia*] *brassicae*), have not been observed. In 1918, however, the rainfall at Perry during July and August was far below normal (table 6, page 971), and in the fall of that year only one fly of a possible third brood was seen. In both 1917 and 1919, third-brood flies were numerous. The absence of a third brood in 1918 might have been due to a lengthening of the pupal period of the second brood caused by the high temperature and low rainfall.

Place of pupation

Puparia of *Hylemyia cilicrura* are usually found near the surface of the ground, a short distance from the place of larval feeding. They are occasionally found as deep as six inches below the surface, but ordinarily not more than three inches below. In bean fields they are often seen within a few inches from the plant food of the larva.

The adult

Emergence

The emergence of what are believed to have been second-brood flies reached its height at Perry, New York, on July 13 and 14, 1917. The flies continued to appear in the rearing cages until about August 1. Flies reared from eggs deposited, no doubt, by this brood and hatching about July 25 and 26, produced, late in August and September, what was possibly a third brood. It is believed that an entire brood of flies was

missed in that year, owing to the delay in opening the laboratory. In that year the spring was very late and the rainfall was heavy thruout June and July.

In 1918 a few females with well-developed eggs were found on May 9. It is not definitely known whether these flies hibernated as adults or were very early specimens of a main brood which came later. Judging from the number of flies taken in the field, the maximum emergence of first-brood flies occurred between May 23 and 26. Second-brood flies appeared in the cages from June 26 to July 5. After July 23 only one fly was found. This was a male, taken on August 26. In that year there were apparently only two broods. The adults came out early in the spring, but, as a result of the hot, dry weather at Perry in late July, either the flies died or the development of the stages of the following brood was retarded.

In 1919 a few flies were found after May 15, but it was not until June 2 that they were at all abundant. They could stil be found easily on June 9, and occasionally until June 17. Most of the females deposited their eggs during the first week of June. Second-brood flies appeared in the cages from June 18 to July 3, with the maximum emergence about June 25. The hot weather of mid-July must have proved fatal to most of the flies, for they disappeared entirely and no more were seen until September 9. Then, for a few days, flies of the third brood were taken. In 1919 there were apparently three broods, or at any rate two and a partial third. The data leading to this conclusion are given in table 3:

TABLE 3. SUMMARY OF RECORDS TENDING TO SHOW THE NUMBER OF BROODS IN 1919

Date		Observations
May	15	3♂, 6♀, taken by sweeping; 2♀ containing well-developed eggs
	20	A few flies taken in an old wheat field
	27	Flies still scarce
	29	2♂, 3♀, taken; eggs small; few flies seen; weather cold
June	2	Flies plentiful; eggs in females ranging from partly developed to mature
	4	Eggs found on decaying material in cages; females in field containing a few mature eggs or no eggs
	9	Fewer flies; abdomens empty
		Small maggots found in beans planted June 2
	11	3♀ taken containing no eggs; abdomens collapsed
	19	First of second-brood flies emerged in cages
	20	13 second-brood ♀ from field examined; eggs undeveloped
	25	Many second-brood flies coming out
July	3	A few second-brood flies still coming out
	15	Weather hot; few flies
	26	No flies seen; flies in cages dead, probably owing to hot weather
Sept.	13	1♂, 3♀, taken on ground plowed for wheat; eggs immature
	15	1♂ taken

In 1920 the first flies were found on May 7, and during periods of warm weather they continued to emerge in numbers until the first of June. Most of the eggs of this brood were deposited between May 25 and June 5. Weather conditions in July of that year were more favorable than in 1919, and flies lived in the cages until the first of August.

Dates of emergence vary greatly at different altitudes. Flies have been found in abundance, a week or more before the Perry emergence, at places ten miles from Perry where the elevation is much less. The bean laboratory was located on what is said to be one of the highest points between Lake Erie and the Genesee River, its elevation being 1400 feet. Data obtained at Perry, therefore, while holding true for much of the western New York bean-growing section, are probably later than for most parts of the State. The opening of spring at Perry is at least a week later than it is at Ithaca.

The time of emergence of *Hylemyia cilicrura* is dependent largely on temperature. If there are several warm days early in May, some flies will appear. If such a warm period is followed by colder weather, additional flies may not be found for a week or two, or until the temperature has again moderated.

Length of life

Adults of *Hylemyia cilicrura* have lived in cages for from 2 to 44 days. In 1920 nine flies under observation lived for an average of 26 days. Without food, life is short, but in cool weather the flies will live for many days in moist cages if they are supplied with sweetened water. The time in this period when eggs are deposited is not well known; but from the fact that adults with immature ovaries are normally found for many days before mature specimens appear, it is probably toward the end of the adult life. Many flies were taken by sweeping in the field on May 20, 1920, at which time most of the females dissected contained immature eggs. Flies taken at this time were placed in cages, and deposited eggs between June 1 and June 6. Apparently, then, the length of the preoviposition period is about two weeks.

Habits

The author's inability to obtain eggs from flies reared in captivity has already been mentioned. Molasses, sugar water, and decaying material were placed in cages, but all failed to supply suitable conditions. A large cage, six feet square, in which beans, cabbage, and mustard were growing and which contained decaying material also, failed to give any better results. Flies were attracted in large numbers by sugar water and molasses. In the field many flies were found in bait pans containing a mixture of molasses, water, and sodium arsenite.

In the spring the flies are attracted to moist, newly plowed ground. They crawl deep into the crevices of the soil, stopping occasionally to lap

up a drop of moisture as they find it. When the flies are moving about in this manner, the wings are overlapped on the back and are thus out of the way. Twelve flies have been counted in three feet of furrow, and forty-two were seen in a square yard. A count of the flies taken on new soil on May 27, 1918, showed fourteen mature females and one male. At this period or a little later, many flies may be taken by sweeping along the edges of fields and roadways. On June 18, 1918, many were caught in the tall grass at the edge of a field, a count showing about four males to every female. On July 8 there were forty-one males in a lot of forty-five flies taken by a roadside. It is apparent, then, that while the females are searching for places suitable for oviposition, the males may be found sunning themselves in grassy and weedy places. On sunny days, adults have been seen resting on mustard; and in the evening they are found on onion tops, kale, potato vines, daisy, and ragweed, and more rarely on other plants. Flies have also been observed hovering about a dead earthworm lying on the surface of the ground.

On warm days, or during the hotter part of the day, the flies are very active, crawling restlessly near the top of breeding cages; but in cold weather they move slowly over the dirt on the floor of the cage, or remain quiet in the cracks of the soil.

It was observed in the spring of 1919 that flies might be taken in the grass along roadsides, and in wheat and oat fields, before they made their appearance around plowed ground. It would seem, then, that as the egg-laying period approaches, flies have a tendency to come into the open and seek loose, moist soil. This is especially true if such soil contains, as an additional attraction, the decomposing roots of clover or quack grass.

HIBERNATION

The writer has little data on the hibernation of *Hylemyia cilicrura*. Cages have been placed in fields and meadows early in the spring, but no flies have emerged in them. Early in May a few flies with ovaries partly mature have been found. It is probable that these were early specimens of the subsequent first brood, which had wintered in puparia; but they may have been flies that had emerged late in the previous summer and had hibernated as adults. It has not been possible to keep flies that are taken in late summer, alive in cages thru the winter. The writer believes that the insects more commonly pass the winter hibernating as second-generation pupae, and emerge as flies from May 15 to June 1 of the next year. Such flies, taken in late May, had only partially developed ovaries and were fresh-looking specimens. In support of this pupal-hibernation theory, N. F. Howard[4] found *cilicrura* hibernating in the pupal stage in onions in Wisconsin, and Dickerson (1910) showed that from pupae of *cilicrura* placed in cages in November, flies would emerge early in May of the next year.

[4] As stated in a general discussion reported in the *Journal of Economic Entomology*, vol. 9, p. 133, 1916.

SEASONAL HISTORY

Adult flies of the first brood are found in the fields from early in May until the middle of June, and deposit their eggs on decaying material or on moist soil about bean-planting time, during the last of May or early in June. The maggots work in beans, corn, potatoes, or rotting vegetation, and emerge as second-brood flies in July. These flies soon disappear in normal hot, dry summers, but apparently they deposit eggs about decaying vegetable matter before they die. A few third-brood flies may appear in August and September, some of which may hibernate; but most of the flies taken in May of the next year are believed to come from the midsummer brood of pupae which overwinter.

CONTROL

Control measures for *Hylemyia cilicrura* may be classed either as artificial, such as seed treatment and the use of baits, or as cultural. The cultural methods involve studies of influential factors in the environment of the insect, and of practices used in growing the crop which may affect the extent of infestation by the maggots. The artificial methods are recorded first.

Artificial methods of control

The studies in artificial control that have been directed against *Hylemyia cilicrura* in the past have been concerned mainly with seed treatments and with the application to the soil of such materials as would either kill the maggots or act as repellents for the adult flies and thus prevent the deposition of eggs. Lintner (1882 a) suggests soaking the seed in gas tar or copperas to keep the maggots away, and Lugger (1896) says these materials work well on a small scale. Headlee (1913) tried solutions of corrosive sublimate, sulfocide, and potassium cyanide, in an effort to kill the maggots and prevent oviposition by the flies, but his results were unsatisfactory. Later (1918) he tells of trying strips of tar, and also of the application of sand treated with carbolic acid to the surface of the soil just after beans were planted. As a result of this treatment, a few more plants came up in the treated plots than in the checks. Still later (1920), Headlee found that a repellent effect on the maggots resulted from treating lima beans with coal tar and dusting them with ashes, lime, or tobacco dust. Chittenden (1909) suggests that carbolic acid might act as a repellent to the adult flies, and both he and Bruner (1910) advise the application of kainit, nitrate of soda, or sulfate or chloride of potash to the soil as a top dressing. In addition to discouraging oviposition, this practice is said to have the added advantage of stimulating plant growth.

While seed treatment and the application of insecticides to the soil may be of value when used in a small way, these practices are of doubtful importance as control measures on a field scale. An infestation of the

TABLE 4. EXPERIMENTS CONDUCTED AT PERRY, NEW YORK, IN 1917, ON SEED AND SOIL TREATMENT FOR THE SEED-CORN MAGGOT

Experiment	Material	Manner of application	Number of seeds planted	Date planted	Date examined	Number of seeds germinated	Number of snakeheads	Remarks
A_1	Hellebore	Drilled in	100	July 12	July 19	78	0	
A_1	Hellebore	Drilled in	50	16	23	20	7	
A_2	Hellebore	On seed	100	16	16	26	2	Hellebore mixed with cottonseed oil
B_1	Iron sulfate	On seed	50	12	19	28	3	2 pounds in 1 gallon of water
B_1	Iron sulfate	On seed	100	16	23	2	1	Flour added as sticker; germination hindered
B_2	Iron sulfate	On seed	50	16	23	5	0	Poured on seed in row
C_1	Borax	On seed	100	12	19	0	0	No germination; radicle injured
D_1	Carbolic emulsion	On soil	50	16	25	22	0	No injury; growth slow
E	Kerosene emulsion	On soil	50	16	25	0	0	Seeds rotted by drench
F_1	Sulfocide (1–1)	On seed	100	12	19	12	0	Cotyledons decayed
F_2	Sulfocide (1–1)	On soil	50	12	19	43	0	Good stand
F_3	Sulfocide (1–1)	In row	50	12	19	45	0	Good stand
F_1	Sulfocide	On seed	100	16	23	22	6	Concentrated material; injury resulted
G_1	Lime-sulfur (1–1)	On seed	100	12	19	20	4	
G_2	Lime-sulfur (1–8)	On soil	50	12	19	35	0	
G_3	Lime-sulfur	In row	50	12	19	0	0	Concentrated material; beans injured
G_2	Lime-sulfur	On soil	50	16	23	17	1	Concentrated material; beans injured
H_1	Dry bordeaux	In row	50	12	19	0	0	Discolored seed coat; germination delayed
H_2	Dry bordeaux	On soil	50	12	19	37	1	Good stand
H_1	Dry bordeaux	On seed	100	16	23	58	1	Good stand
H_2	Dry bordeaux	In row	50	16	23	43	1	Good stand
H_3	Dry bordeaux	On soil	50	16	23	45	1	Good stand
I_1	Creosote	On seed	100	12	19	0	0	Beans rotted
J_1	Quassia solution	On seed	100	16	23	30	3	Normal spray solution, hop-aphis strength
J_2	Quassia solution	In trench	50	16	23	17	2	
K_1	Black-leaf-40 (1–100)	On seed	100	12	23	0	0	Seed decayed
K_2	Black-leaf-40 (1–100)	On soil	50	16	23	12	2	Slow growth
L_1	Sulfur	In trench	100	16	23	28	7	
M_1	Tobacco dust No. 1	On seed	50	16	23	10	1	Slow growth
M_2	Tobacco dust No. 2	On seed	50	16	23	1	0	Slow growth
R_1	Scalecide (1–15)	On seed	100	16	23	25	8	
R_2	Scalecide (1–15	On soil	50	16	23	20	4	
	Check		100	12	19		4	
	Check		100	12	19		8	
	Check		50	12	19		4	
	Check		100	12	19		3	
	Check		100	16	23		11	
	Check		100	16	23		8	
	Check		100	16	23		4	
	Check		100	16	23		2	

seed-corn maggot cannot easily be predicted; its first indication to the grower is usually the discovery of the maggots in beans that have failed to germinate. Since this is true, an efficient repellent or seed treatment would have to be used every wet year, which would make the cost for material and labor very high. Furthermore, it is difficult to find a material which does not injure the seed and yet has a killing or repellent effect on the insect. Maggots usually enter the bean between the cotyledons, and therefore, after the seed coat, which bears the treatment, is broken or cast off by the swelling of the seed, the tender plumule is again left unprotected.

The writer has tried various materials as control measures, on a small scale, in the hope of finding something suitable for larger tests. The results of these experiments are recorded in table 4.

In the experiments reported in table 4, the materials were placed either on the seed coat, on top of the soil, or in the row with the planted seed. These experiments were located in fields where bad infestations of maggots had just been found and where the flies were very numerous. Infestations were not large, however, as the plantings came between broods. Dry bordeaux mixture seemed the most promising of the materials tested, but on the whole the results of experiments in 1917 were not encouraging.

In 1920, seed- and soil-treatment experiments were again conducted. A part of the experimental field which had not been under cultivation for several years, and which was covered with quack grass, was plowed, and the experiments were started here on June 4. At that time many females of *H. cilicrura* were mature and had been depositing eggs for several days. Beans were planted, following a rain of 0.25 inch, on June 3. It was noted that the flies had been more numerous on this part of the field than on the other parts which had been previously under cultivation, showing the attraction of the species to turned-under quack grass as a place for oviposition. Snakeheads, the evidence of maggot attack, were much more abundant here than in the main part of the field when counts were made on June 22. The results of the experiments of 1920 are given in table 5.

None of the materials tested in 1920 gave promise of success in practical use. While in a few cases the number of injured plants was reduced, in no case did the seedlings entirely escape harm. Taking into consideration the difficulty of predicting infestations of the seed-corn maggot, it seems to be unwise to rely on control measures of this type in New York.

The bait of sodium arsenite, water, and molasses, which was tried against the onion maggot by Sanders,[5] was tested against *H. cilicrura*. On June 21, 1917, the material was sprinkled on the soil with a whisk broom, and pie tins containing it were placed in a row across the field. Flies were very numerous in this field and the second planting of beans had just been made, the first seeding having been destroyed. On the morning of June 22, twenty-nine flies were found in the pans, together with many beneficial

[5] As stated in a general discussion reported in the *Journal of Economic Entomology*, vol. 8, p. 89, 1915.

TABLE 5. EXPERIMENTS IN 1920 ON CONTROL MEASURES FOR THE SEED-CORN MAGGOT

Experiment	Material	Manner of application	Number of seeds planted	Number of seeds germinated	Number of snake-heads	Number slightly injured	Per cent of beans injured		Remarks
							In relation to those germinated	In relation to those planted	
Check	.....	.....	50	35	5	2	*20*	*14*	.....
A	Sulfur.....	In row.....	100	58	16	5	36	21	.....
B	Sulfate of potash.....	In row.....	100	52	14	6	38	20	.....
C	Calcium cyanamid.....	In row.....	100	23	4	1	21	5	Burning resulted
D	Nitrate of soda.....	In row.....	100	5	2	1	60	3	Burning resulted
Check	.....	.....	50	39	7	1	*20*	*16*	.....
E	Acid phosphate.....	In row.....	100	58	16	2	31	18	.....
F	Floats.....	In row.....	100	68	12	5	25	17	.....
G	Ammonium sulfate.....	In row.....	100	14	2	0	14	2	Injury resulted
H	Ground limestone.....	In row.....	100	71	7	3	14	10	.....
I	Nitrate of potash.....	In row.....	100	28	7	0	25	7	Growth slow
Check	.....	.....	50	39	8	0	*20*	*16*	.....
J	Dried blood.....	In row.....	100	40	10	1	27	11	.....
K	Gypsum.....	In row.....	100	68	21	2	33	23	.....
L	Dry bordeaux.....	In row.....	50	36	8	0	22	16	.....
Check	.....	.....	50	35	10	5	*42*	*30*	.....
M	Tobacco dust.....	In row.....	100	68	14	4	26	18	.....
N	Kerosene and lime.....	On soil.....	100	39	3	0	7	3	Growth delayed
O	Carbolic emulsion (1–20)...	In row.....	100	50	3	2	10	5	.....
P	Tarred sand.....	On soil.....	100	41	0	2	5	2	Injury resulted
Q	Arsenate of lead (2–50).....	On seed.....	100	66	5	3	12	8	.....
R	Bordeaux paste (4–4–50)...	On seed.....	100	66	2	2	6	4	.....
S	Lime-sulfur (1–20).....	On seed.....	100	65	6	1	9	7	.....
Check	.....	.....	100	65	5	4	*14*	*9*	.....
T	Carbolic and lime.....	In row.....	100	60	6	1	8	7	.....
U	Creosote and lime.....	In row.....	100	19	2	0	10	2	Injury resulted

carabid beetles. No dead flies were seen in the field outside of the pans, and later, when the beans came up, there was no reduction in the number of snakeheads near the pans. Pans were placed in other fields, and, tho many flies were captured, no great benefit was noticeable when the beans were examined two weeks later.

Before planting was done in this field, which was very wet, the seed was drenched with kerosene. Eight days after planting, the counts showed 49 maggot-infested seeds out of 110 that were examined. When the seed was treated overnight with carbon disulfid, 17 out of 57 beans contained larvae of *H. cilicrura*. A check had 28 infested seeds in 50. Altho neither material injured the germination of the seed, there was little if any repellent effect produced.

Beans were treated also with arsenate of lead in the form of a strong paste. This was allowed to dry and the seed was then placed in the ground with a bean planter. The poison so injured the seed that only about 15 per cent germinated. A check showed an 85-per-cent stand.

Neither seed treatment nor other artificial control measures have given promise of success. No satisfactory material has been found, and nothing that looks promising for tests on a large scale has been discovered.

Natural and cultural methods of control

There are many factors bearing on the presence or the absence of *Hylemyia cilicrura* in a field. Some of these are discussed in the following pages, and practices which are in the nature of preventives are pointed out.

Moisture and temperature as factors in the life of the seed-corn maggot

Hylemyia cilicrura has been found to be a serious pest in New York when the early summer is rainy. This increased injury in moist seasons is apparently due to the tendency of the cultivated hosts to decay in the wet soil, thus becoming attractive to the flies as a place for oviposition. It seems probable, also, that maggots already in the soil feeding on other decaying vegetation, are attracted to the beans when they begin to decay.

In June of 1916 and also of 1917, the rainfall far exceeded the normal. In 1917 the June rainfall (6.4 inches) was more than twice the monthly average for the previous twenty years, and the damage from *H. cilicrura* was severe in all the bean-growing sections of the State. July of that year was rainy also, and thruout that month flies could be taken easily, altho normally they are scarce at that season. The years 1918, 1919, and 1920 were nearly normal, and the loss was slight. In table 6 are given data from the United States Weather Bureau at Rochester, New York.

In periods of drought such as prevailed at Perry during July and August of 1918, flies are difficult to find. By July 22, 1918, only six flies of many hundreds were still alive in the cages, and on the following day not a fly

could be found in the field. On August 26 one male of *H. cilicrura* was taken, and this was the only fly seen in 1918 after July 22. The conditions at Perry in that year were abnormal, for this region suffered much more for want of rain than did the surrounding places. The reduction in the number of flies appearing at Perry in 1919 is possibly due to this prolonged dry period.

TABLE 6. TEMPERATURE AND MOISTURE RECORDS OF THE UNITED STATES WEATHER BUREAU AT ROCHESTER, NEW YORK, DURING THE SUMMERS OF 1917 TO 1920, INCLUSIVE

(Records of marked variations from the Rochester records found at Perry are given in bold-faced type)

Month	Mean temperature (Fahrenheit)					Rainfall (inches)				
	1917	1918	1919	1920	Normal	1917	1918	1919	1920	Normal
May	49.2°	61.7°	56.4°	55.8°	56.7°	3.16	1.75	5.20	0.78 **2.01**	2.94
June	62.8°	62.6°	72.8°	65.7°	66.1°	6.40	2.40	2.96	1.15	3.13
July	71.7°	70.2°	72.2°	67.8°	70.4°	4.23	2.70 **1 03**	3.40 **1.21**	2.93	3.09
August	69.0°	71 5°	67.8°	70.3°	68.3°	2.51	1.83 **1.34**	3.60 **5.70**	1.51	2.96

In July of 1919, the rainfall at Perry was again below normal, and the flies in the cages died rapidly after July 1. Between July 1 and July 20, the rainfall was only 0.67 inch, and the maximum temperatures for this period ranged from 65° to 96° F. After July 15 no flies were seen for two months and the specimens in cages all died. August of that year had nearly twice the normal rainfall.

The temperature early in the summer appears to have an influence on the abundance of *H. cilicrura*. In 1917 the mean temperature for May was 49.2°, which is several degrees below the average for the month and is the lowest recorded since 1871. The maggots and flies during that season were the most numerous in the history of the insect. June temperatures in 1917 also were lower than the normal, and had been each year since 1913.

H. cilicrura is an insect which in the past has been injurious for one year, or for a few successive years, and has then become of negligible importance for an indefinite period. This variation is undoubtedly connected to some extent with the moisture and temperature conditions of the early summer. Moderately low temperatures with an abundant rainfall in the spring appear to be favorable to the insect, while dry, warm weather during the summer is detrimental to its successful development. A succession of cold, wet years brings forth the insects in greatest numbers.

Relation of time of bean planting to time of oviposition

Eggs may be deposited by *Hylemyia cilicrura* near decaying vegetable matter in newly plowed or recently fitted soil before the beans are planted, while they are being planted, or even after planting. In rare instances a combination of these two possibilities may be found. When the eggs are deposited previous to planting, the maggots feed on decaying matter in the vicinity for a while, becoming nearly full-grown before they enter the bean seed; but when the eggs are deposited subsequent to planting, small larvae will be found in the beans within a few days after they are planted.

As examples of oviposition in the soil before the beans are planted, the following instances may be mentioned. In the experimental field at Perry, in 1919, one piece was plowed on May 14 and planted on May 28. When it was examined on June 5, many full-grown maggots were found. Allowing ten days for the larval period and two days for the egg stage, the eggs were probably deposited about May 24. A field that had been in alfalfa for several years was plowed for beans in May. Planting took place on June 6 and 7, and when the field was examined on June 12 the maggots present were ready to pupate. These maggots were hatched from eggs deposited probably about June 1. Maggots of about the same size were found in the old alfalfa roots.

As illustrations of egg-laying either at the time of planting or subsequent to it, the following examples are given. In 1919 a field of beans was planted on June 2. When it was examined on June 9, maggots a few days old were found. Flies were very common in the field on June 2 when the seed was drilled in. Beans were planted in a test plot on the experimental field on June 5. On June 10, when these were examined, some contained newly hatched maggots. In a field in Niagara County beans were planted on June 9. Small maggots were found feeding on the plumule leaves on June 14.

In the rainy year of 1917, when *H. cilicrura* could be found everywhere, fields were inspected late in June. Small and large maggots were found in the beans, pupae were in the soil, and flies with eggs in all stages of development were hovering over the ground. It is only late in the spring of very wet years that all stages can thus be found simultaneously. In more normal years the flies seem to appear in roughly defined broods, and the heavy oviposition of each brood does not extend over a period of more than a week.

From the foregoing data it is evident that a grower cannot be sure that maggots are not already working on other matter in the soil at the time when he plants his beans. Moreover, if mature flies are numerous at planting time, his beans may be infested with maggots from eggs deposited at that time.

In 1919 an attempt was made to connect the time of fly emergence and the time of oviposition with some of the more obvious occurrences in

nature. In that year, and also in 1920, the first flies were taken in small numbers early in May, about the time when cherries were in bloom. Mature flies were out in numbers near plowed ground on June 2, 1919, at which time the last of the petals had fallen from late apple trees at Perry. Flies with fully developed eggs had not been found in quantities on plowed ground before this, altho a few females with immature eggs had been collected in winter-wheat and oat fields. Many eggs were deposited in cages about June 4. Dissected females showed that some eggs were mature on June 2 and many on June 4. It is evident, therefore, that under Perry conditions in 1919, beans planted between June 2 and 12, or within ten days after the last of the petals had fallen from the late apple trees, were open to maggot attack. Serious infestations of maggots were very few in 1919, but in two bean fields which did show *cilicrura* injury the seed was planted on June 5 and June 6, respectively.

On May 28, 1920, when the petals had partly fallen from the late apple trees, flies nearly mature were found in numbers on moist, newly turned ground, especially where the field had previously been in sod. After May 7, when the first specimens of the year were taken, adult females were captured almost daily and their abdomens examined for eggs. Between May 7 and May 28, a few flies with ripe eggs were occasionally found, showing that eggs were doubtless deposited in small numbers during that period. A cornfield planted on May 22 and examined on May 29 showed typical *cilicrura* injury in a few seeds. However, this examination of females taken thruout May showed that most of the first brood of flies were not mature before May 28. At that time there were many more females than males present on plowed ground. Many eggs were deposited between May 28 and June 7 by flies in the cages. Most of these eggs were deposited after June 1, when the nights as well as the days were warm and the flies showed unusual activity.

Many fields in which beans were just appearing above ground were examined on June 7, 1920, and only six infested plants were found. Good weather had made it possible to plant some of these beans by May 21, and all were in before June 1. Therefore, in these fields, the seed was in the ground before most of the flies were mature, with the result that there were but few maggots in the soil.

Beans planted in the experimental field on June 4, 1920, were heavily infested, and potatoes and corn planted in neighboring fields about the same time contained many maggots. This infestation is probably due to the fact that the seed was put into the ground at the time when the flies were mature and eggs were being deposited. Beans planted in the middle of June were uninjured. From these data it would seem that beans planted just after the last apple blossoms have fallen, which under the conditions at Perry in 1919 and 1920 was from May 28 to June 7, stand a greater chance of being infested by the maggots of *H. cilicrura* than do those planted

before or after these dates. Since the larvae already in the soil may attack the newly planted seed, it is wise to delay planting for a few days after all the eggs have been deposited. This would extend the time for probable infestation in 1919 and 1920 from May 28 to about June 15. Unfortunately, it is not always possible to choose the time of planting as suggested above. Weather conditions may prevent planting in May, before the flies are mature, and if beans are put in too late in June they may not ripen before they are killed by frost. Seasons vary so much from year to year that no absolute rule can be given; but, if weather permits, it is best to plant before the oviposition period of the flies, when the last of the petals have fallen from late apple trees.

Relation of kind and condition of soil to maggot infestation

Abundant moisture provides favorable conditions for the development of *Hylemyia cilicrura*, as is shown on page 970. Beans on heavy soil, which holds moisture, grow more slowly, decay, and furnish conditions attractive to the flies for oviposition. In 1917 one side of a bean field near Perry was badly infested, while the remainder, which was planted on the same day, was free from injury. An examination of the soil in the infested part showed it to be heavy and sticky, while the unattacked beans were growing in lighter soil of a sandy constituency, which was relatively dry. The division between the two types of soil was very marked, and the good and the poor beans followed this line closely. Well-drained fields are not attacked as often as are those where the drainage is poor. Low and wet spots, where water may collect in otherwise good fields, often yield poor beans. This is in part the result of maggot work, but it may often be due to the decay caused by the excess of moisture in the soil.

Warm, dry soil that is well fitted furnishes ideal conditions for the growth of beans. In soil of this kind they will germinate quickly, and when once above ground there is little chance of serious injury from maggots. In wet seasons it is best to delay planting until the soil can be well fitted. A field should be dragged and rolled, and the top layer of earth allowed to dry out and become warmed by the sun.

Influence of preceding crop and time of fitting a field, on maggot attack

Heavy infestations of *Hylemyia cilicrura* have been found on land that had previously been in potatoes, corn, tomatoes, wheat, oats, and beans, as well as in clover and alfalfa sod. Many infestations have followed sod, since the upturned roots of decaying clover and alfalfa furnish good breeding conditions for maggots, and since clover forms a part of a regular rotation of beans, wheat, and clover which is practiced in western New York. Just as serious outbreaks have been found, however, where the preceding crop was beans, especially if the field had an abundance of quack grass and weeds. In the writer's garden there was a patch of quack grass. This was turned under, and beans and peas planted on

this spot were infested with maggots, tho in other parts of the garden there was no injury.

Whelan (1916) has found maggots in fresh manure, and he says:

> Furthermore, it appears that while beans were apt to suffer when planted on freshly turned clover sod, especially if recently fertilized with undecomposed manure, they stood a much better chance of escape if the field was prepared early in the season and the maggots given a chance to develop and disappear before the beans were planted.

Tho the writer has been unable to find evidence of flies breeding in manure, he has found many maggot-infested fields which had been covered with manure just before plowing. It must be said, however, that serious outbreaks have been found where manure was not used.

If a field is fitted early and is allowed to dry out before the mature flies seek places to oviposit, it appears to be less attractive for oviposition than newly turned soil. In 1920 the laboratory field was plowed at a time when flies with well-developed eggs were numerous, and many bean seedlings were infested. Fields near by that were plowed earlier and allowed to stand were free from maggots.

Relation of depth of planting to injury by maggots

Beans planted deep in the ground take longer to reach the surface and are thus exposed for a longer period of time to maggot attack. It has been observed many times that beans planted deep in wet ground suffer more from *Hylemyia cilicrura* than those that are planted less deep. For example, in 1917 it was often noticed that the headlands yielded better beans than the remainder of a field. This is attributed to the more shallow planting, for the soil was not so loose at the edges of the field and therefore the drill did not sink so deep.

In 1917 a field under observation had nearly every bean attacked by maggots. The seed had been planted in wet soil at a depth of from three to five inches. After this first planting was destroyed by maggots, the field was reseeded at once, and the beans were dropped as near the surface of the ground as possible. Some of the seed was even left on top of the soil, and a boy with a hoe followed the machine to cover the beans left exposed. A 95-per-cent stand resulted.

In another case a grower started to make a very shallow planting of beans. When he had gone part of the way across the field, he decided that he was not getting the seed in deep enough, and so he planted the remainder of the seed much deeper. At harvest time the beans planted first, the shallow-planted ones, were the only ones worth harvesting. If the beans are planted too deep, many will decay because of the excessive moisture, and the maggots will destroy a large proportion of the remainder

Experiments were conducted in 1917 to test the effect of the depth of planting on the time required for the beans to break thru the soil. Beans were planted on good, tho very wet, soil on July 12. When the field was

examined on July 19, the beans that were planted about one inch deep were nearly all up, those planted three inches deep were about half thru the soil, and none of those planted five inches deep were yet above ground. In another wet field 100 seeds were planted at depths of one, three, and five inches, on July 16. On July 23 there were, in the one-inch planting, 57 plants, of which 4 were snakeheads; in the three-inch planting there were 35 plants, of which 5 were snakeheads; and none of the beans planted five inches deep had appeared above ground. In the laboratory field, under rather warm, dry conditions in July, 1918, it was found that beans planted three inches deep came up nearly as quickly as those planted more shallow.

Summary of preventive measures

The results of experiments on artificial control measures, such as coating the seed before planting and treating the soil with materials of a repellent nature, afford small hope for their future successful development. As a result of a study of some of the factors governing infestations, the possible preventive measures that have been discussed in the foregoing pages are summarized in the following paragraphs.

The seed-corn maggot is more serious as a pest when the months of May and June are rainy, and the ground is cold and wet at bean-planting time, than under other conditions. The greatest injury results when several unfavorable years occur in succession. *Hylemyia cilicrura* thrives when oviposition takes place under wet conditions; and therefore it is wise to plant when the soil is dry and the earth is warm. The soil should first be well fitted with a disk or a harrow, and then rolled, and finally, after a few warm days have dried out the top soil, the beans should be planted. If the field is fertilized in order to hasten the germination of the seed, there is a still better chance of getting a stand. However, fields fertilized with fresh manure just before plowing often show a heavy infestation of maggots, and so this condition should be guarded against in wet years.

As maggots developing from eggs deposited on newly tilled ground are often found in decaying matter in the soil, it is sometimes wise to fit a field early, before most of the flies are sexually mature. The ground will then be dried and less attractive to flies for oviposition by the time they come out. The presence of many flies of this species crawling over newly turned soil between plowing and planting time is a good indication that seed planted there will probably be infested. In 1918, 1919, and 1920, sexually mature flies were most numerous in the fields at Perry from May 25 to June 10. In 1919 the greatest number were present about June 4, and in 1920 about June 2. If the weather permits, it is better to plant ahead of this brood. If this is impossible, planting should be delayed until the flies are less common.

It is extremely important that beans should not be planted too deep in wet soil. If they are, some of the seed will rot and the maggots will destroy

most of the remainder. Not only is the soil three or four inches below the surface much colder and more moist than the top inch, but also the deeply planted seed germinates more slowly in wet years. It is wise to force seed to germinate and grow as rapidly as possible, since it will have escaped serious injury when it is once above ground. If in shallow planting some of the beans are left on top of the ground, they may easily be covered with a hoe. A bean planter or a corn planter usually will give better service than a drill in wet years, for either is lighter and will not sink so deep in wet places. If a drill is used, it should be adjusted to make a shallow planting. A grower who plants his seed deep in wet soil at a time when the sexually mature flies are numerous, is sure to have a heavy infestation of maggots on his beans.

THE IMPORTED FIELD GRAY SLUG
(*Agriolimax agrestis* L.)

ORIGIN

The field gray slug, or garden slug (*Agriolimax agrestis*, Plate LXIX, 6), is an imported species which, with two other foreign forms (*Limax maximus* L. and *L. flavus* L.), does more damage and attracts more attention than all of the other twenty-nine species of slugs reported from the United States (White, 1918). *A. agrestis* is an old res dent of Europe, having been listed in England as early as 1674. Taylor (1907) reports it in the fossil rocks of the Pliocene and Pleistocene periods from many places in the British Isles, as well as from Germany and France. It apparently came to this continent from Europe early in the eighteenth century.

HISTORY AND DISTRIBUTION

Theobald (1905) states that *Agriolimax agrestis* is found in near'y every garden in England, and also on the continent of Europe and in Siberia, Madeira, and Algeria. Taylor (1907) states that it occurs also in Turkestan, China, Japan, Asia Minor, Morocco, Cape Colony, Zanzibar, Australia, and New Zealand, as well as in Brazil, Jamaica, and parts of Canada, on this continent.

In the United States it was first reported near the seaports of Boston, New York, and Philadelphia. De Kay (1843) states that Binney knew it before 1843, tho Binney (1851) still had trouble in separating *A. agrestis* from the native species *A. campestris*, which it very much resembles. Since 1851 *A. agrestis* has spread gradually westward, and it is now found locally in many States. Its presence is reported in the literature of Maine, Massachusetts, New York, Pennsylvania, Michigan, New Jersey, Illinois, Wisconsin, Ohio, Colorado, Washington, and California, but it is probably present also in many other parts of the country. Slingerland discovered the slug at work on the college farm at Ithaca in 1891. Baker

(1902) did not find it around Chicago in 1902, tho it had been reported from Michigan in 1899. Cockerell[6] found *agrestis* in Colorado in 1890, and he states that it was brought there from New Jersey. He reports it also in Oregon in 1891 and in California in 1892.

In western New York the localities infested by *A. agrestis* are increasing, and in wet seasons many beans, as well as other field and garden crops, are injured. The insect is apparently not a pest in all sections of the bean-growing counties, but appears to be limited to a few farms and gardens in each district. Some places seem to be entirely free from it. It is often abundant on small truck farms, and around the shrubbery and the gardens in city lots. It has, no doubt, been carried into its present habitats in the straw or moss packing of bulbs, shrubs, or nursery stock. Disseminated in this way, it seems to thrive, and it apparently prefers cultivated crops to woods and pasture land. As it becomes better established the species may be expected to spread from the present centers of infestation until it is of almost general distribution. The long, cold winters often experienced in New York, however, should tend to prevent the serious damage that it causes nearly every year where the climatic conditions are milder and more uniformly moist.

SYSTEMATIC POSITION

The field gray slug belongs to the phylum Mollusca and the class Gastropoda, which includes the slugs and the snails. *Agriolimax agrestis* is placed in the family Limacidae, the members of which have no external shell. This family, according to Pratt (1916), is represented in America by only six species. The large spotted slugs of the family are now placed in the genus Limax L., while smaller forms, such as *agrestis*, belong in Agriolimax Morch. Because of its varied coloration, this slug has been described under many specific names. Taylor (1907) gives a complete synonymy for the species, and lists ten varieties, with the localities from which each has been reported.

GENERAL DESCRIPTION OF THE SLUGS OF THE FAMILY LIMACIDAE

The field gray slug belongs to the same group of Mollusca as the snails, and differs from them but little except in the size and form of the shell. In slugs of the family Limacidae no shell is visible on the outside of the body, but there is a thin calcareous plate (Plate LXIX, 5) concealed in the mantle — the fleshy shield over the front part of the slug. The body is elongate-subcylindrical, and bears a more or less prominent dorsal keel. On the retractile head are two pairs of tentacles; the anterior pair aids in feeding, while the upper, or posterior, pair bears the eyes. The eyes have the form of rounded knobs on filament-like stalks. When the slug is disturbed,

[6] As cited by Taylor (1907:120).

the eyes may be withdrawn down the tentacle, and in young, transparent specimens they may be readily seen even after they have been retracted into the head. Slugs have the power of secreting from pores in the body, and especially from the anterior ventral surface of the foot, a slimy substance known as *mucus*. The shell-concealing mantle has, near its posterior lower border on the right side, a circular breathing pore which opens into a respiratory chamber beneath. This is lined with a richly vascular epithelium subserving the function of a respiratory organ. Just behind the right eye-stalk is the opening of the genital organs, thru which eggs are extruded. Slugs of this group are hermaphroditic, both male and female genital organs being present in a single individual.

ANCIENT SUPERSTITIONS CONCERNING SLUGS

Slugs have been known in Europe for many years, and the older writings in regard to them contain many interesting notes. They have been used as food in Europe, and it is said that as late as 1863 they were prescribed by French physicians, to be taken in the form of a sirup. A slug distillate was considered good for the complexion (Kingsley, 1885). A plaster of slugs with the heads removed, bound on the forehead, was believed to cure a headache, and slugs eaten alive in milk were thought to cure consumption (Rogers, 1908).

As slugs always appear after a rain, they were believed by English farmers in the eighteenth century to come from heaven in a rain cloud (Theobald, 1895). Since toads gather in infested fields to feed on the slugs, it used to happen that gardeners and farmers of a hundred years ago, finding that their plants had been destroyed during the night, would blame and kill the toads, while the real culprit was concealed in a safe retreat under ground (Ritzema Bos, 1890). Later, the value of toads as enemies of the slugs was appreciated and three francs a dozen was paid for them (Guénaux, 1904). Years ago the small shell of the slugs was regarded as an amulet, which, worn on a string around the neck, was believed to protect the wearer from harm. When the slugs suddenly appeared in large numbers in the gardens of European countries, it was customary to invoke the power of the Church against them, in the hope that they might be thus removed (Kingsley, 1885); and Taylor (1907) states that the Ritual of Paris, A. D. 1712, contains definite exorcisms for this purpose.

PECULIAR HABITS OF SLUGS

Some slugs are said to have a partiality for moist newspaper, dead fish, earthworms, dead clams, dead slugs, meal, flour, cream, butter, Pears' soap, sponge cake, and book bindings, as food (Cooke, 1895). They have been known to eat out the corks of wine bottles, to crawl into nearly empty beer bottles and bathe themselves in the contents, and even to attach their small mouths to the dripping faucets of containers of

alcoholic beverages. They will crawl into beehives and feed on the honey, apparently immune to the stings of their enraged hosts (Reh, 1913).

ECONOMIC IMPORTANCE

In wet years the field gray slug is one of the two most destructive animal pests of field beans in New York. During the rainy summers of 1916 and 1917, nearly all of the plants in some fields were attacked and many were entirely destroyed. Estimates of the losses on twenty-one farms in Orleans County in 1917 varied between 5 and 70 per cent. In 1918 the writer saw a bean field in Monroe County in which about one-third of a ten-acre field was so badly attacked that not a trace of a plant was left above ground.

In addition to its attacks on field beans, the slug often causes much injury to garden beans, lettuce, cabbage, peas, potatoes, radishes, and strawberries. As the species becomes better established in the farms and gardens in new localities thruout New York, it is probable that more widespread attacks may be expected on crops during wet seasons.

NATURE OF THE INJURY TO BEANS

Immature specimens of *Agriolimax agrestis* eat the tender tissue between the veins and the veinlets of the leaves, thus giving them a skeletonized

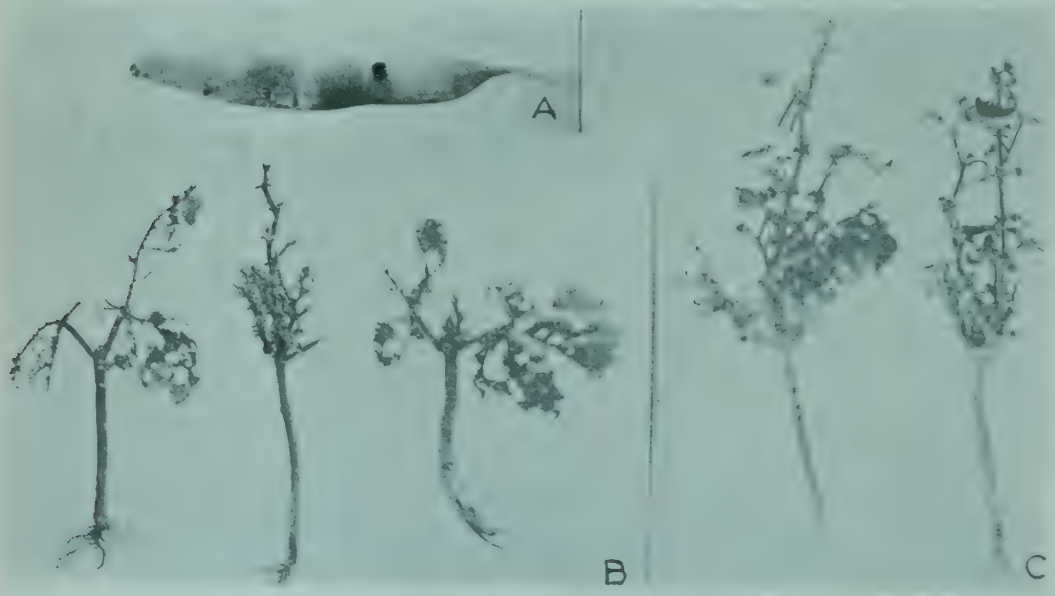

FIG. 91. INJURIES CAUSED BY AGRIOLIMAX AGRESTIS

A, A bean pod showing a hole made by the slug in feeding. B, Bean plants injured by slugs. (Photographed in midsummer.) C, Bean plants that were injured by slugs soon after they appeared above ground, photographed at harvest time.

appearance. Older slugs, however, eat parts from the edges of the leaves, and frequently continue to feed until every leaf is devoured (fig. 91, B).

FIG. 92. RADULA OF AGRIOLIMAX AGRESTIS, AND RESULTS OF WORK OF SLUG

A, Radula, or lingual ribbon, of slug, made up of many hundred small, sharp teeth, × 25. B, Young bean plants showing result of feeding by the slug. C, A bean field in Monroe County, New York, in parts of which all the plants were destroyed by slugs; bare areas shown.

Sometimes the petiole and a few of the main veins are left, but oftener the entire plant above the surface of the ground is destroyed. During

the daytime and in dry weather the slugs feed beneath the ground, eating large parts of the stems of plants (Plate LXX, 2, and fig. 92, B). Such plants may be so severely injured that a wilting of the parts above ground results.

When a slug crawls up the stem of a young bean plant, it usually devours the budlike growing tip before it moves on to the leaves. Plants of this kind are always stunted and show an abnormal, useless growth of small leaves (fig. 91, C). Such plants commonly die, and even when they survive they fail to produce mature seeds.

If the slugs are numerous at the time of pod formation, it is not unusual for them to eat holes into the sides of the pods (fig. 91, A) and feed on the soft beans within. Often several holes of this kind are found in a single pod, and sometimes a slug after destroying one bean will move along inside the pod and feed in turn on all the remaining seeds.

INJURY TO PLANTS OTHER THAN BEANS

In its nocturnal feedings above ground, *Agriolimax agrestis* seeks the tender leaves of lettuce, corn, cabbage, and cauliflower. The injury which the slug does to these plants is similar to that which it produces on large bean leaves, and causes the plants to become unhealthy and unmarketable. When the weather is such that the slugs are active in late summer, they frequently eat large holes in the sides of ripe tomatoes and fall strawberries, in addition to eating the leaves.

The pest feeds underground on potatoes, and, together with the millepede *Julus caeruleocinctus* Wood, causes considerable damage in western New York by eating out large cavities in the tubers. Carrots, turnips, radishes, and beets suffer similar attacks on their fleshy roots.

HOSTS AND POSSIBLE FOOD SUPPLIES

Agriolimax agrestis has such a wide range of food plants that it is classed as almost omnivorous. Among the plants which it feeds upon are cabbage, potatoes, eggplant, lettuce, beans, lima beans, peas, corn, strawberries, gooseberries, cucumbers, melons, cauliflower, wheat, turnips, beets, carrots, radishes, celery, clover, oats, dahlia, dandelion, dock, chicory, tobacco, hops, and tomatoes. There are also many weed hosts on which this mollusk may be found, such as burdock, ragweed, lamb's-quarters, and mustard. It finds palatable several species of mushrooms also, and many ornamental shrubs and vines, and it finds abundant food in sod land and in lawns Overgrown places in fence corners and along the edges of fields often harbor many of the slugs. Manure is acceptable to them as food, and their eggs, as well as young slugs, have been observed in large numbers where manure had been scattered in piles around a field. Cooke (1895) mentions as among the possible foods of *agrestis*, may-flies, beetles, and dead

slugs; Lovett and Black (1920) add sow bugs, earthworms, and aphids to this list; Taylor (1907) records a case in which *A. agrestis* killed and ate slugs of the species *A. campestris* when the two were placed in the same box; and Lebour (1914–15) finds that they eagerly devour the proglottides of Moniezia, a tapeworm of sheep. It would seem, therefore, that, while the slugs usually prefer a vegetable diet, under some conditions they relish animal food.

DESCRIPTION OF STAGES

The egg

The egg of *Agriolimax agrestis* (fig. 87, C, page 954) is elliptical or spherical in shape, and is translucent, jelly-like, bluish white, and iridescent. Under magnification the thin outer covering is found to be slightly roughened with regular raised and depressed areas. The eggs are found either singly or in masses, in the latter case being held together by a transparent secretion. On one end the small, projecting micropyle is visible, especially in newly deposited eggs. The eggs vary from 1.6 to 3 millimeters (1/16 to 1/8 inch) in length.

The young slug

A newly hatched specimen of *Agriolimax agrestis* is without definite form at first, but it soon assumes much the same appearance as its parent except that its tentacles are relatively larger and its body is transparent, permitting the black nerve cord running to the eye to be easily seen thru the body covering. Young slugs have a pinkish tint at first, but later turn to darker hues as they begin feeding.

The full-grown slug

The slug (Plate LXIX, 6, and fig. 87, D) is described by Taylor (1907:105) as follows:

> Animal limaciform, with large but flattened tubercles; of a somewhat uniform whitish or pale ochreous ground colour, but sometimes dull lavender or other tint, often mottled, speckled or reticulated with brown or black, and at times totally suffused with black; body somewhat compressed and keeled towards the tail; tentacles dark coloured; shield more than one-third the total length of the animal, rounded in front and behind, concentric striae not deep, with the nucleus on the right side and towards the rear; respiratory orifice with a broad usually unpigmented raised ring, which is cut anteriorly by the anal cleft; sole pale and longitudinally tripartite, the side areas sometimes darker, especially towards the tail; sole-fringe separated as usual from the body by a furrow, containing a row of elongate tubercles, upon which the body tubercles rest unconformably. Mucus plentiful and viscous, often clear when crawling, but becoming milky-white on irritation, due to innumerable particles of carbonate of lime.
>
> Length usually about 35 mill.

LIFE HISTORY AND HABITS

The egg

Under New York conditions, some of the eggs of *Agriolimax agrestis* are deposited in the fall, from August until December, and many of the mature slugs die soon afterward from the cold. If full-grown slugs live thru the winter, they may deposit eggs during May and June of the following spring. Slugs developing from these overwintering and spring eggs will mature and in turn deposit eggs in the fall of that year or in the following spring.

In the summer of 1917, which was very wet, eggs were deposited more or less continuously from May to December, being especially numerous in September and October. Theobald (1905) reports this to be the normal condition in England. Lovett and Black (1920) state that in Oregon egg-laying occurs at all seasons of the year, and that the greatest number of eggs are deposited in the spring and early summer.

In 1918, which was a drier and more nearly normal season for New York than the preceding years had been, eggs were deposited by the slugs in cages during May and June, and not again until September 23. In that year, as well as in 1919, most of the eggs were deposited late in October and during November. Moisture is a factor of great influence. A few of the eggs deposited in July and August of 1917 hatched that fall, but whether these young slugs survived the cold winter that followed is not known.

The dates of hatching for eggs deposited on May 4, 1918, by an overwintering slug were as follows: May 27, three; May 29, two; June 1, four; and June 2, five. The average length of the egg stage was 26.5 days. Eggs that had been deposited late in the previous fall hatched between May 10 and June 6, the length of the egg stage in this case being between six and seven months. Early in the summer all the slugs in the fields are about the same size, and it is therefore probable that the fact that some eggs are deposited in the spring and others in the fall has little influence on the hatching date

During the winter of 1917–18, there was in the greenhouse, where the temperature ranged from 55° to 75° F., a wide variation in the length of the egg stage, which ranged from 26 to 57 days, the average for 189 eggs being 37.3 days. In a greenhouse which was kept at a constant temperature of 80° F., 24 eggs hatched in an average of 24.3 days. Theobald (1905) gives from three to four weeks as the normal egg stage in England.

The eggs of *A. agrestis* are tucked into crevices of the soil, not far below the surface of the ground, and are also hidden under rubbish and projecting stones, around the walls of buildings, and among the roots of grass. In bean fields that have been badly infested, the slugs collect under the bean piles in the fall and deposit many eggs. In the fall of 1917 more than five hundred slugs were taken under a pile of this kind, and the eggs were

countless. Slugs thrive in sod land and many eggs may be found in the spring around the roots of grass in fence corners and in meadows.

One pair of field gray slugs may deposit from 500 to 800 eggs, according to Theobald (1905). This writer says that the eggs are given out in batches of about 50 at a time, cemented together in piles of from 6 to 15. Taylor (1907) cites a case in which a pair of *agrestis* deposited 774 eggs during the season, and Lovett and Black (1920) found 612 eggs deposited by one specimen between May and the following April. One slug, found by the writer early in the spring, deposited 180 eggs between May 5 and June 19. Two slugs confined in one cage have produced as many as 464 eggs before they died, and it is probable that, due to cage conditions, this was less than the normal number.

Many eggs of *A. agrestis* do not hatch. After the severe winter of 1917, the writer was unable to find a single egg in the spring where there had been thousands in the fall preceding. This natural destruction is, without doubt, a great help in reducing the numbers of the pest in western New York. While the eggs need moisture for their development, excessively wet surroundings are unfavorable, for under such conditions they become moldy and spoil tho they may retain their normal shape. In a dry environment, the egg covering will shrivel and the egg will contract until it might be mistaken for a particle of the dirt on which it rests. When moisture is added, however, it will again swell to normal size. Bland and Binney (1873) describe experiments in which eggs of *A. agrestis* were dried many times in a desiccator, in some cases being kept in this condition for several years; when these eggs were again placed in normal moist surroundings, they assumed their usual shape and hatched. Since the development of the embryo in the egg is easily observed, much study has been given to this part of the life cycle by Mark (1881), Kofoid (1895), and Byrnes (1899).

The young slug

Newly hatched specimens of *Agriolimax agrestis* differ but little in their habits from the full-grown slugs. Because of the limited food supply in proportion to the large number of slugs hatching from a single egg mass, these slugs appear gregarious. As they become older and more hardy, they migrate from the original center and spread out in search of other food. Cooke (1895) reports that on hatching they go into the ground for four or five days before feeding. The writer had noted that green food in cages did not show strong evidence of feeding for several days after the slugs hatched, but he had attributed this to the small size of the radula, or rasping organ, at this time.

The young slug often secretes its slime in such large quantities that it is able to descend from plants to the ground on a thread of this material. Taylor (1907) states that this slime thread is the same as the trail left by the slug wherever it crawls, except that it is freed from contact with the

earth. The same writer declares that *agrestis* is able to descend at the rate of five inches a minute on a thread of this kind, and that one specimen was found hanging on a thread seven feet from the point of attachment. At times they reascend by this same thread.

The full-grown slug

The adults of *Agriolimax agrestis*, as well as the young, are nocturnal. They are seen during the day only in cloudy or rainy weather, or in shady and concealed places. In an infestation under observation on July 13, 1918, the slugs were on the plants from seven o'clock in the evening until eight in the morning. As it becomes light, the slug crawls into a crevice of the soil or under some protective covering such as grass, straw, or boards. This aversion to light is said to continue even after the eye-bearing tentacles have been removed. In a bean field the slugs frequently burrow down near a bean plant and feed on the parts below ground. The writer has found them buried from four to eight inches deep in the soil, with their tentacles drawn in. They were contracted and inactive, and were covered with a coating of slime to which particles of dirt adhered. In the cold weather of winter they hibernate in this resting position.

The field gray slug moves by an almost imperceptible shortening and lengthening of the muscles of the foot, or under side of the body. Taylor (1907) declares that two inches a minute is a good speed for this species, and has estimated that at this rate it would take twenty-two days and ten hours of steady movement to cover a mile. Since the slugs have been in this country they have apparently absorbed some of the American spirit, for they have been observed to go much faster than this. Some slugs are reported to return to the same hiding place night after night, but *agrestis* apparently does not have this habit.

The nocturnal travels of the slug are recorded each morning by the trail of slime which the animal leaves wherever it goes. After a rain these slime trails are often found on sidewalks, and in heavily infested fields the writer has seen the ground and the plants so coated with this glistening secretion that they have an iridescent appearance. More slime is secreted on a dry surface than on one that is moist, and on the dry surface the slime appears more milky, due, it is believed, to the presence of particles of carbonate of lime. This mucous secretion is supposed by some writers to aid in locomotion, while other writers declare that it regulates the evaporation, thus controlling the body temperature. It is thought also to serve as a protection against enemies. When irritated by a finely pulverized substance, such as lime, *agrestis* will give off large amounts of slime from the pores of its body, and when this mixes with the powder it usually forms a coat around the animal. The slug is sometimes able to escape by leaving this coat behind, but it may become so weakened by its struggles that it dies within the covering.

Method of feeding

Agriolimax agrestis does not eat in the same manner as does a biting insect, for its feeding apparatus is very different. The jaw (Plate LXIX, 10) is a concave, chitinous process attached to the roof of the pharynx. In the center it bears a tooth with finely serrate edges, which helps in tearing food apart. Opposed to this, on the floor of the pharynx, is a flexible plate made up of many small, sharp teeth, known as the radula (Plate LXX, 1, and fig. 92, A, page 981). This radula, or lingual ribbon as it is sometimes called, is supported on the muscular tongue and may be moved forward and backward. By the combined use of jaw and radula, small particles of food are torn from a plant and are then passed on to the stomach. Cooke (1895) states that the teeth of the radula are sharp enough to break the skin of the human hand if the slug is permitted to use this organ for a short time in one place.

Mating and oviposition

It has been previously noted that *Agriolimax agrestis* is hermaphroditic, both male and female sexual organs being found in the same individual. Whether or not the slugs are capable of self-fertilization is not definitely known. Theobald (1905) says that self-fertilization is rare, and that the male and female reproductive organs mature at different times. In the winter of 1917–18 the writer isolated specimens of *agrestis* a few days old and kept them in breeding jars in the insectary. One slug, on reaching maturity, deposited a few eggs; but because of an accident to the heating plant at a time when the temperature was far below zero, these eggs were frozen. Since that time it has been impossible to obtain eggs from isolated specimens, and therefore it cannot be said whether eggs of this type are fertile.

On the evening of July 7, 1920, the writer saw for the first time the sexual union of *A. agrestis*. Two specimens, one much larger than the other, were crawling around and around each other on a patch of slime about an inch in diameter. Sometimes they would strike each other with their tentacles. Soon the excitatory organ, or sarcobelum, was extruded, and this also was used in a caressing manner. After this behavior had continued for about three-quarters of an hour, the sarcobelum of each slug enlarged very greatly; the two organs came together and there was a great discharge of slime. In regard to the actual transfer, Taylor (1907:107) says, "The seminal element, mixed with mucus and worked up into a little ball, is transferred bodily, the forerunner of a true spermatophore."

Time required to reach maturity

In ordinary years, under field conditions in New York, slugs that have developed from eggs hatching in May are ready for oviposition in October

of the same year. This makes the time to sexual maturity about five months. In the wet season of 1917 this period was shortened to three months for some individuals. When the slug overwinters, it may be more than twelve months before it begins to deposit eggs.

Many specimens of *Agriolimax agrestis* that hatch in the spring do not live thru the following winter under New York conditions. In no case have slugs under observation lived thru two winters. This would make the greatest length of life actually observed in New York about eighteen to twenty months.

In European writings it is stated that *A. agrestis* may live for several years (Theobald, 1895); also, that the slugs are sexually mature in six weeks, and that there may be several generations in a year (Reh, 1913). Cooke (1895) reports that slugs of this species are usually full-grown by the middle of the second year and die during the first part of the third year. Taylor (1907) cites one instance in which a slug mated and deposited eggs in sixty-six days, was full-grown in eighty-two days, and lived for about eighteen months. The same writer states that the time from hatching to maturity probably varies from ninety days to nearly one year.

NATURE OF OUTBREAKS

When the outbreaks of *Agriolimax agrestis* occurred in 1917, it was noted that ordinarily the bean fields were evenly attacked. All the plants showed some injury to leaves and vines, but only a few were completely destroyed. The exception to this was in a field where a large tree, with its border of sod, seemed to act as a center from which the slugs migrated. In the grass near this tree were found many eggs and adults of *A. agrestis*, showing the place to be the local seat of infestation.

Only one outbreak of *agrestis* was observed by the writer in New York in 1918, and that was in Monroe County, in a slightly rolling field where the knolls had been covered with horse manure in the preceding fall. This field had been in sod for several years. The infestations seemed to start from the knolls, and when the field was seen by the writer the plants had been entirely destroyed as far as the slugs had migrated (fig. 92, C, page 981). Leaves and vines were completely devoured and the parts below ground were also attacked. The infested area grew larger each night as the slugs moved forward along the rows. In this infestation slugs of all sizes were present; the larger ones (40 millimeters) were in the front ranks of the advancing hosts, while far back in the devastated part of the field were the small ones (4 millimeters), which had been left behind in the rapid advance. This variation in size is unusual in New York and was probably the result of the exceptionally good hibernating place provided by the manure and sod of the field, which no doubt had allowed more or less continuous development thruout the winter.

RELATION OF AGRIOLIMAX AGRESTIS TO MOISTURE

Agriolimax agrestis is a moisture-loving animal. It is found above ground in large numbers only after rains or on cloudy days when the relative humidity is high. In 1916 and 1917, wh ch were damp years at Perry, the slugs of this species were unusually active in the bean fields. During the past three years there have been no extensive, general outbreaks. From an examination of the relation of the rainfall of the past four years to the abundance of the slugs, it would seem that rainy weather in May and June, when the eggs are hatching and the young slugs are beg nning their growth, makes conditions most favorable for their development. Especially is this true if two or more such years come in succession. In 1916, and again in 1917, these months were rainy. In June of 1916 the rainfall at Rochester, New York, was 5.72 inches, and for the same month in 1917 it was 6.40 inches; while in 1918, 1919, and 1920, it was below the monthly average of 3.13 inches.

It sometimes happens, after a rainy period, that the ground dries and bakes so hard that the slugs cannot break the hard crust and are thus forced to feed below the surface. On heavy, undrained soils the damage is always greater than on lighter ground. Since the growth of the slugs is dependent on the amount of food eaten, and since their feeding is heavier in moist surroundings, it is easy to see why they mature much more quickly in moist than in dry seasons. During dry periods the slugs are found deep in the soil, in contracted positions. They work their way far below the surface of the soil in search of moisture. Reh (1913) says that a slug supplied with plenty of moisture after having been under dry conditions, may become three times as large as it was before.

RELATION OF AGRIOLIMAX AGRESTIS TO EXTREMES OF TEMPERATURE

The field gray slug can survive cold weather if it is in a protected position; but a temperature of −14° F. proved fatal to specimens in flower-pot cages in the insectary at Ithaca when there was no fire in the building for several days. Few slugs survived the unusually cold winter of 1917–18, as was shown by the fact that in the spring of 1918 the writer could find but a small number in the fields near Perry where there had been thousands in the fall preceding. The slugs that had escaped the cold had done so by crawling under the sod and the rubbish in fence corners or other protected places. Very few of the millions of eggs deposited under the bean piles in the fall of 1917 survived. These occasional severe winters are believed to have an important influence in keeping down the numbers of this pest in New York. January of 1918 was the coldest January, as well as the coldest month, within the scope of the official weather records. The mean monthly temperature for that month at Ithaca was 9.7 degrees

(Fahrenheit) below the normal. The first half of February was also unusually cold. Since that year slugs have been so scarce that injury to beans caused by them has been almost unheard of.

In the study of the distribution of *Agriolimax agrestis*, it may be noted that it has not been reported as serious in the Southern and Middle Western States. This is perhaps because the high, dry temperatures of these States during the summer are unfavorable to its successful development.

SEASONAL HISTORY

In western New York there is normally but one generation of *Agriolimax agrestis* in a year. Sometimes the eggs deposited in the fall hatch in the following spring, and the slugs from these eggs are full-grown by August and, in their turn, deposit eggs from September to December. These adult slugs usually die before the next spring. Sometimes, however, full-grown slugs live thru the winter and deposit their eggs in May and June of the next year. These spring eggs hatch at about the same time as the overwintering eggs.

PREDATORY AND PARASITIC ENEMIES

In England, acording to Theobald (1905), slugs are preyed upon by the thrush, the starling, the pigeon, the blackbird, the duck, and poultry, as well as by the toad, the shrew, the mole, and the centipede. Ritzema Bos (1890) states that in France, beetles of the families Carabidae, Staphylinidae, and Lampyridae feed on slugs; and Cooke (1895) reports that there is a fly which lays its eggs with those of *Agriolimax agrestis*, and that the slug is parasitized by the larva. The same writer says also that nematodes likewise help to reduce the numbers of these slugs. Banks (1915) reports that a mite (*Ereynetes limaceum* Koch) has been found attached to some species of slugs.

In western New York, chickens free to run in the fields have eaten many slugs. Eggs of the species in a wet petri dish were found to have nematodes feeding in them. The small worms would apparently make a hole thru the outer covering of the egg and feed on the embryo within.

CONTROL

Various control measures against *Agriolimax agrestis* have been tried and recommended. In many cases advantage has been taken of the irritation and the secretion of mucus caused by finely pulverized and granular materials coming in contact with the slug. Lime, both air-slaked and hydrated, is the most commonly recommended of these irritants; other materials suggested are salt, caustic soda, tobacco dust, wood ashes, soot, road dust, hellebore, powdered coke, sawdust, and various combinations of these.

Slugs are very often trapped by placing cabbage leaves, straw, culled potatoes, turnips, sacking, or shingles near their favorite haunts in the evening. In the morning they may be easily found and destroyed under these traps, where they have crawled to avoid the daylight. Poison baits of bran, chopped green leaves, drippings, and potatoes, mixed with arsenate of lead, white arsenic, arsenite of zinc, arsenate of calcium, or paris green, as the poison, are said to help in slug control. Fertilizers such as land plaster, nitrate of soda, potassium sulfate, and iron sulfate have been recommended, especially in European countries.

For killing *A. agrestis* by contact or for controlling the slug by a repellent, it has been advised that plants be sprayed with blue vitriol solution, with bordeaux mixture, with pyrethrum, or even with hot water; and as a poison, a spray of arsenate of lead or calcium arsenate is suggested.

It is thus evident that many methods of control have been advised, some of which may work well in a small garden. In a bean field of ten acres or more, with an even infestation thruout, the problem is one of greater complexity.

Experimental work

When this study was begun, in the summer of 1917, the easiest method of control appeared to be the application of a poison spray to the plants. Experiments along this line were started on July 17. Several rows were

TABLE 7. CONTROL EXPERIMENTS AGAINST AGRIOLIMAX AGRESTIS

Material applied	Effect on slugs
Very fine tobacco dust	Dead in 15 minutes
Coarse tobacco dust	Not killed
Builder's lime	Dead in 5 to 15 minutes
Dry powdered bordeaux (dust)	Dead in 5 to 60 minutes
Tobacco dust, sulfur, arsenate of lead (1–5–1)	Dead in 15 minutes
Sulfur (finely ground)	Not killed
Copper sulfate (10-per-cent solution)	Dead in 15 minutes
Copper sulfate (5-per-cent solution)	Dead in 40 minutes
Copper sulfate (2-per-cent solution)	Not killed
Sulfocide (5 cc. to 500 cc. of water)	Not killed
Lime-sulfur (1–20 solution)	Not killed; irritation caused
Black-leaf-40 (1 cc. to 500 cc. of water)	Dead in 2 hours
Quassia solution (hop-aphis formula)	Not killed
Lime (air-slaked)	Dead in 3 to 20 minutes
Washing soda (dust)	Dead in 10 minutes
Chloride of lime (dust)	Dead in 15 minutes
Washing soda (1 pound in 3 gallons of water)	Not killed
Chloride of lime (1 pound in 3 gallons of water)	Dead in 2 hours

sprayed with a mixture of 3 pounds of powdered arsenate of lead to 50 gallons of water. No difference could be noticed between the sprayed and the check plots when they were examined some time later. Slugs were placed also on sprayed plants in cages. Feeding was noticed on the leaves but the animals were not killed. In the greenhouse, in December of 1917, a slug devoured two heavily sprayed plants and lived for many days. From these data it seems evident that ordinary doses of arsenate of lead do not kill *Agriolimax agrestis*.

The experiments summarized in table 7 were carried on in the insectary at Ithaca during the winters of 1917 and 1918. The slugs were sprayed with the liquid or were dusted lightly with the powder, after which they were returned to natural conditions, on moist earth in an open jar.

It may be seen from table 7 that under insectary conditions many dusts proved effective. Copper-sulfate solution also showed strong killing power. It was noticed at this time that a 10-per-cent copper sulfate solution, sprayed on a piece of paper and allowed to dry, was very irritating and sometimes fatal to a slug that crawled across the paper. Lime, chloride of lime, and washing soda were more effective in the form of dust than in the liquid form. Approximately ten slugs were used in each test.

The experiments summarized in table 8 were likewise conducted in the insectary during the winters of 1917 and 1918. Bean plants growing in a bench, and also the ground close to them, were treated with the various liquids and dusts, and a cylinder open at the top was placed over them.

TABLE 8. Control Experiments against Agriolimax agrestis

Material applied	Effect on slugs
Hydrated lime water (1 pound to 3 gallons)	1 killed, 1 kept from plant for one week
Stone lime (1 pound in 2 gallons of water)	Killed in trying to reach plant
Bordeaux (4–4–50)	Chose unsprayed in preference to sprayed leaves
Arsenate of lead (2 pounds in 50 gallons of water)	Alive after eating two plants
Arsenate of lead, as above, sweetened with molasses	Molasses injured plant
Calcium arsenate (1–50) and sulfocide	Slug not killed; little feeding
Calcium arsenate (1–50) sweetened	Molasses injured plant
Sodium arsenate (10 grams in 1 gallon of water)	Slug alive; plant killed
Check (sprayed with water)	Slug alive
Kansas grasshopper bait	3 of 4 slugs alive 1 week later
Salt and lime (1–10)	Slug killed in 24 hours
Iron sulfate (10-per-cent solution)	Plant killed
Arsenate of lead and lime (1–8)	Slug kept from plant for 1 week
Hellebore and lime (1–25)	Slug killed in 2 hours

One or more slugs were then placed in the cylinder at some distance from the treated plant.

In the experiments summarized in table 8, the repellent effect of bordeaux mixture is shown. Hellebore and lime, as well as salt and lime, showed some killing power under insectary conditions. Calcium arsenate and lead arsenate when sweetened with molasses were fatal to the bean plants, and the ineffectiveness of arsenate of lead as a stomach poison of *A. agrestis* is shown.

In the summer of 1918, contact substances, in powder form, were tried against *A. agrestis* near the field laboratory at Perry. The material was dusted lightly on the slug with a Niagara duster and the animal was then returned to natural conditions. Five slugs were used in each test. The results of some of these experiments are given in table 9:

TABLE 9. EXPERIMENTS WITH POWDERED-CONTACT SUBSTANCES AGAINST AGRIOLIMAX AGRESTIS

Material applied	Effect on slugs
Superphosphate	Killed slowly if extensively used
Rock phosphate	Killed slowly if extensively used
Acid phosphate	Killed slowly if extensively used
Basic phosphate	Not killed
Land plaster	Not killed
Fine ground bone	Not killed
Sulfate of potash	Killed quickly
Nitrate of soda	Killed quickly
Dried blood	Not killed
Ground limestone	Not killed
Calcium cyanamid	Killed rather slowly
Kainit	Killed quickly
Salt	Killed quickly
Sulfur	Not killed
Fine tobacco dust	Killed slowly if extensively used
Chloride of lime	Killed very quickly
Air-slaked lime	Killed quickly
Water-slaked lime	Killed quickly
Salt and lime (1–10)	Killed very quickly
Hellebore and lime (1–10)	Killed very quickly
Hyposulfite of soda	Killed slowly

The nitrate of soda and the kainit proved injurious to the plants when tested in the field. Of the dusts that were not injurious to the plants, as recorded in table 9, the salt-and-lime and the hellebore-and-lime combinations, and the chloride of lime alone, acted the most rapidly, altho some of the other materials also showed killing power.

Liquid-contact materials also were tested in 1918, as shown in table 10. While the slug was crawling on the ground it was sprayed with the liquid from an atomizer, and was then left under natural conditions.

TABLE 10. Liquid-Contact Sprays Tried against Agriolimax agrestis

Material applied	Effect on slugs
Black-leaf-40 (1–400), soap (4–50)	Killed slowly but surely
Limewater (2-per-cent solution)	Killed
Chloride of lime (2-per-cent solution)	Killed quickly
Kerosene emulsion (10 per cent)	Not killed
Kresco sheep dip (10 per cent)	Killed
Carbolic emulsion (1–20)	Killed
Copper sulfate solution (5 per cent)	Killed slowly

In the experiments summarized in table 10, ten large slugs were used to test each material. The Black-leaf-40 was fatal every time, but it often required several hours to kill the slug. The limewater, the chloride of lime, and the carbolic emulsion proved fatal in thirty minutes. The copper sulfate seemed to work much more slowly than in the former tests.

In 1918, during an outbreak at Charlotte, New York, a poison bait composed of one quart of chopped clover, one teaspoonful of arsenate of lead, and one tablespoonful of molasses, was tested. The slugs showed no preference for this bait, and several specimens that were placed where the bait was the only food available, and thus forced to eat it, were not killed.

In July, 1920, the writer was able to find a sufficient number of slugs to enable him to conduct a small series of laboratory tests. The result of these are given in table 11.

In the experiments of 1920, recorded in table 11, both full-grown and immature slugs were used. It was noted that the larger individuals often revived from doses that proved fatal to the smaller specimens. Control materials in dust form seemed to give much better results at this time than did the same material applied as a liquid. In previous experiments sprays have sometimes seemed to give as favorable results as the dusts. There is apparently some varying factor that enters to either help or hinder the killing power of some of these materials. It is possible that the relative humidity may have some influence. Black-leaf-40, which had shown good killing power in the previous experiments, seemed to act very slowly even at the increased strength that was used. Carbolic-acid emulsion gave satisfactory results, and when applied to bean foliage it caused no injury under the prevailing conditions. The best results at this time came from

the contact dusts, but when lime was applied to slugs in the field it was necessary to use several doses before killing resulted. The slug would give off the usual slime, which would mix with the lime to form a coat from which the animal soon freed itself. Heavy doses often killed when light applications did not.

TABLE 11. CONTROL MATERIALS TESTED AGAINST AGRIOLIMAX AGRESTIS IN 1920

Material and strength	Number of slugs	Effect on slugs after 18 to 24 hours
Liquids:		
Black-leaf-40 (1–250), soap (4–100)	25	Small slugs killed if sprayed heavily; large ones revived
Black-leaf-40 (1–250), glue (1 pound to 50 gallons)	10	Small slugs killed; a few large ones revived
Glue (4 pounds to 50 gallons of water)	10	Not killed
Black-leaf-40 (1–250), lime (1 pound to 3 gallons) (light dose)	10	Sick, but all except one revived
Same (heavy dose)	10	All killed
Hydrated lime (1 pound to 3 gallons of water) (light dose)	10	All alive next day
Air-slaked lime (1 pound to 3 gallons of water) (heavy dose)	10	Two large slugs alive; remainder dead
Same (light dose)	10	Five large slugs alive
Lime (1 pound to 3 gallons of water), salt (1.6 ounces to 3 gallons)	10	Five large slugs alive
Lime (8 ounces to 3 gallons of water), chlorinated lime (1.6 ounces to 3 gallons)	10	One large slug alive
Lime (8 ounces to 3 gallons of water), caustic soda (1.6 ounces to 3 gallons)	10	Four large slugs alive; plants burned
Chlorinated lime (8 ounces to 3 gallons of water)	10	Five slugs alive
Carbolic emulsion (diluted 1–30)	10	Killed quickly
Lye (2 pounds to 50 gallons of water)	10	Killed quickly; plants killed
Resin – caustic soda wash (28.3 g. resin, 3.5 g. caustic soda, 645 cc. water)	10	Four small slugs killed
Dusts:		
Hellebore and lime (1–25)	10	All dead
Chlorinated lime and lime (1–25)	10	All dead
Hydrated lime	10	All dead
Niagara Sprayer Company's "All-in-One"	10	All dead
Water-slaked lime	10	All dead
Salt and lime (1–10)	10	All dead
Caustic soda and lime (1–20)	10	All dead
Sulfate of potash	10	All dead; plants burned
Calcium cyanamid	10	All dead; plants burned

Three field cages, containing bean plants sprayed, respectively, with powdered arsenate of lead (2 pounds to 50 gallons of water), calcium arsenate (1 pound of the powder to 50 gallons of water), and water alone to serve as a check, were set up in the laboratory field in July, 1920. Twenty slugs were placed in each cage. The plants sprayed with arsenate of lead were freely eaten, as had been the case in previous experiments; but those sprayed with calcium arsenate showed little evidence of any feeding after the first two days. Several dead slugs were found in the calcium-arsenate cage, while none were found in the arsenate-of-lead cage. The check plants, sprayed with water only, were almost entirely destroyed. The scarcity of slugs in the field had made it impossible to test the calcium-arsenate spray on a larger scale.

A cage was placed in the field covering eight bean plants on July 7, 1920. Four of these plants were sprayed with bordeaux mixture and four were left unsprayed. Twenty slugs were then placed in the cage. A week later the unsprayed plants were badly eaten, while the sprayed plants were almost untouched. Only where a leaf had been missed by the spray was it injured.

Since the above work was carried on, the excellent paper of Lovett and Black (1920) has come from the press. As a result of many careful experiments, these writers conclude that, for Oregon conditions, a spray of bordeaux mixture (4–4–50) as a repellent, supplemented by a poison bait of calcium arsenate (one part by weight to sixteen parts of chopped lettuce), is the most effective means of slug control. When lettuce is not available, cabbage, kale, clover, or other succulent leaves may be used. The writers say that this bait should be scattered in small heaps at frequent intervals over the infested area. The importance of cleaning up crop remnants and débris about fields and gardens is also emphasized. In an experiment testing the efficiency of this combination of repellent and poison bait, Lovett and Black found 33 out of 35 slugs dead at the end of twenty-four hours. The bordeaux had kept the slugs from the plants and they were killed by feeding on the poison bait.

As previously stated, the severity of the winter of 1917–18 apparently killed many hibernating slugs and many slug eggs. Few slugs have been found in New York bean fields since that time, and the writer has not found conditions favorable for control experiments in the field. In 1920 there were more slugs in bean fields than in the two preceding years, but very little injury resulted. The control work has therefore been limited to field-laboratory and greenhouse experiments carried on whenever slugs were available. Results of laboratory experiments have at times been contradictory, and, since laboratory control measures often prove entirely inadequate in field practice, it is impossible at this time to do more than suggest possible control measures for field use under such conditions as those of western New York.

The repellent quality of bordeaux mixture appears to be definitely established. Plants sprayed with bordeaux have escaped all injury when unsprayed plants were entirely devoured. It has been demonstrated by Lovett and Black (1920) that calcium arsenate also has great killing power when used in a poison bait, and the writer found dead slugs in a cage in which the beans had been sprayed with this material. It is therefore reasonable to suppose that a spray of calcium arsenate may be effective under field conditions.

Dusts of lime, salt and lime (1–25), hellebore and lime (1–25), and chloride of lime and lime (1–25), show some promise of success, and on a small scale should work especially well.

A very helpful practice, both in field and garden work, is to remove all rubbish and crop remnants from the ground. Old bean and potato vines, cabbage stumps, carrots, turnips — in fact, decaying vegetation of any kind which may furnish either food or shelter for the slugs — should be cleared away. Straw, boards, roots of quack grass, piles of leaves, and manure, have been found to harbor many of the pests. After a slug infestation, crop remnants should be plowed under or removed from the field as soon as the crop has been harvested. It is advisable also to clean up the edges of gardens and fence corners in the fall if slugs have been abundant during the summer, for the greatest injury to the plants is that caused by slugs hatched from the eggs deposited by overwintering slugs that have hibernated in these places. After the grass and the weeds have been cut and the rubbish has been removed, the application of a heavy coating of lime or salt to the ground helps to destroy the animals.

Beans grown in fields that were in sod the preceding year are often infested. Covered by the roots of the grass, the slugs and their eggs have been well protected during the winter, and when spring comes they find an abundant food supply in the newly planted beans. If manure is added in the fall to sod land in which slugs are present, it makes hibernating conditions even more ideal.

Summary of control suggestions

Bean plants should be thoroly sprayed with bordeaux mixture (4–4–50) to keep the slugs from them. The plants should be sprayed from both above and below, preferably with a potato sprayer having three nozzles to a row. Unless the infestation is severe, this spray should be sufficient. In severe attacks, however, the bordeaux mixture may be supplemented by a bait of chopped lettuce or clover, 16 parts by weight to 1 part of calcium-arsenate powder, the mixture to be scattered around the field. This bait should attract and kill slugs driven from the plants by the bordeaux. As an experiment, the bean foliage may be sprayed with calcium arsenate, 1 pound to 50 gallons of water. In a small garden the slugs

may be collected at night, by the light of a lantern; cabbage leaves, shingles, or straw may be used as traps, from which the slugs may be collected in the morning and destroyed. All crop remnants and rubbish should be carefully removed from infested areas in the fall and destroyed, and salt or lime should be scattered around the edges of the infested fields or gardens. Manure should not be placed on infested fields or gardens in the fall.

HOW TO DISTINGUISH THE VARIOUS SPECIES OF SLUGS FOUND IN BEAN FIELDS

There are three slugs that the writer has frequently found associated with *Agriolimax agrestis*. They are *Agriolimax campestris* Binney, a native species, and *Limax maximus* L. and *Arion circumscriptus* Johnson,[7] imported species. The following key may help in distinguishing the four species.

A. Body blunt or rounded at posterior end; respiratory opening in anterior half of mantle; back not keeled in mature forms; color gray, with a black lateral band the entire length of body; length 30 mm..... *Arion circumscriptus*

B. Body pointed at posterior end; respiratory opening in posterior half of mantle; back with at least a small keel at posterior end; color varied, but without the single lateral stripe.

a. Slug large (100–200 mm.); spotted or with longitudinal bands of black. *Limax maximus*

b. Slug smaller (25–50 mm.); color uniform or mottled.

aa. Ground color usually whitish or ocherous, mottled or speckled with brown or black; mantle pore with unpigmented border; tubercles flattened; slime milky; length when full-grown, 50 mm..... *Agriolimax agrestis*

bb. Color uniformly amber or black; mantle pore of same color as remainder of mantle; tubercles not flattened; slime watery; length when full-grown, 25 mm..... *Agriolimax campestris*

Agriolimax campestris Binney

Animal limaciform, with large, not flattened, tubercles. Color uniform grayish or amber, often black. Body somewhat compressed and keeled toward the caudal end. Tentacles dark-colored. Shield more than one-third total length of animal, rounded in front and behind. Respiratory orifice not differing markedly in color from remainder of mantle. Sole dark and longitudinally tripartite. Mucus clear and watery. Penis spiral. Length about 25 mm.

Agriolimax campestris, a native species, is closely related to *A. agrestis*. It differs from *agrestis* in being smaller, darker, and of a more uniform coloring. While *agrestis* seems to collect in large numbers and to thrive on cultivated crops, *campestris* is more inclined to be solitary and to frequent woods and meadows. In April, full-grown *campestris* are often found under stones or in sod, and the eggs have been found at the same time. Eighteen of these eggs, taken on April 22, hatched between May 21 and June 1. The young of *campestris* are darker than the young of

[7] Determined by H. A. Pilsbry.

agrestis, some being almost black. It is not uncommon to find *campestris* feeding on beans, but they never occur in numbers large enough to seriously damage the crop.

The spotted garden slug, Limax maximus L.

Limax maximus (Plate LXX, 6), is described by Taylor (1907:35) as follows:

> Animal with a long and slender body, tapering towards the tail, and varying in length from 100 to 150 mill., but occasionally reaching to even 200 mill.; usually of a yellowish-grey or cinereous ground colour, variously banded or maculated with black, but sometimes unicolorous; body rounded, but keeled towards the caudal end, with about forty-eight longitudinal rows of elongate, detached tubercles; neck pale, with two conspicuous dorsal furrows enclosing a single row of elongate tubercles and terminating in front as the facial grooves; sole uniformly pale; foot-fringe pale with a row of minute submarginal blackish tubercles; tentacles very long and slender; shield oblong, about one-third the total length of the animal, rounded in front, angular behind, and forming an angle of about 80 deg. when in motion, usually of a similar tint to the body, but boldly marbled or maculate with black, somewhat concentrically and interruptedly ridged around a sub-posterior nucleus. Mucus colourless and ridescent, not very adhesive.....

Limax maximus is a large slug, of the family Limacidae, which has been imported into this country. It is found in the British Isles, and thruout Continental Europe, South Africa, and Australia. It has been in America for many years and may be found locally in many parts of New York State, where it frequents greenhouses, hedgerows, woods, and damp, shady places. It occurs also in and around houses occasionally, when it has been carried in on vegetables that are stored in the cellar. Taylor (1907) states that the slug is almost omnivorous, having been known to relish beans, tobacco, flowers of many kinds, cauliflower, fungi, custards, milk, bread, raw and cooked meat, fruit, and sugar.

L. maximus has a keen sense of smell. It has been known to crawl, in the dark, straight to a plate of meat that was six feet away. The position of the plate was then changed three times, and each time the slug altered its course accordingly. It is said that *L. maximus* often returns to the same spot night after night, after its wanderings in the dark. The progress of the night's journey is shown by the slime trail which is left wherever the animal goes.

Arion circumscriptus Johnson

The following description of *Arion circumscriptus* (Plate LXIX, 12) is taken from Taylor (1907:228):

> Animal of the *Arion* shape, but stouter especially when contracted.....about thirty mill. in length when adult and fully extended; of a pale creamy-grey colour, darker grey dorsally, but shading to whitish towards the fringe; a black and sharply-defined lateral band extends the whole length of the body on each side, beneath which is sometimes an indistinct orange band, formed by pigment cells breaking through the skin; there is a slight mid-dorsal keel when young, which, however, gradually disappears during growth, but its place is almost

invariably indicated by a line of pale mid-dorsal tubercles, which contribute to form a pair of dorsal or inner bands; shield granulose and bluntly rounded at both ends, bearing a disconnected continuation of the longitudinal body banding; body tubercles rather long and slender; sole opaque, waxy white, and indistinctly tripartite, the median portion slightly darker and more transparent than the side areas, and occupying more than one-third of the width of the body; foot-fringe broad and white or pale-grey in colour, usually without perceptible lineolations, but sometimes the lineoles are clearly pigmented, especially at the caudal end of the body.

Another slug occasionally found with *Agriolimax agrestis* in New York is *Arion circumscriptus* Johnson, a species imported into this country from Europe and reported by Taylor (1907) from Niagara Falls and from the District of Columbia. The writer has found it very common at Ithaca, at Perry, and at Waterville, in New York. This slug apparently prefers to live in sod land, in decaying tree trunks, or under fallen leaves. It may be found in grassy orchards, feeding on bruised and decaying fruit. It is seldom, if ever, injurious to growing plants. The species belongs to the family Arionidae. It may be easily separated from the other slugs found with *Agriolimax agrestis* by the position of its respiratory pore, which is in the anterior half of the mantle while in the other forms it is in the posterior half. A longitudinal black band runs the full length of the animal's body.

THE PALE-STRIPED FLEA BEETLE

(*Systena taeniata* Say)

The pale-striped flea beetle, *Systena taeniata* (of the family Chrysomelidae), is found in the bean fields in New York State every year, in large or small numbers. This small, active insect is brownish yellow in color, with a broad yellow stripe running lengthwise along each wing cover (Plate LXIX, 11). There are several color varieties of the insect, but the common one in New York is *blanda*, in which there is little contrast between the stripe and the remainder of the wing cover. The typical dark form is found occasionally. In early writings these varieties were often treated as separate species. When *S. taeniata* is numerous in dry summers, the beetles may cause considerable injury to beans by attacking the foliage. They leave in their wake many shallow feeding places on the surface of the leaves, and some of these spots later develop into irregular holes. If the plant is unable to supply sufficient soil water for the increased transpiration resulting from the injury, the leaves will turn a sickly yellow. In a year when the normal supply of soil moisture is available, beans can sustain much damage from the feeding of the insect without any serious injury resulting to the development of the plant.

S. taeniata is a well-known insect in nearly all parts of the United States, and in many places is considered a serious pest. It has injured sugar beets in Michigan, in New York, and in Colorado, corn in Illinois, clover in Kentucky, cotton in Georgia, Kieffer pear grafts in Maryland, and seedling apple trees in New York. Other host plants of the insect are

cabbage, potato, pea, tomato, pumpkin, melon, squash, cucumber, turnip, radish, carrot, eggplant, strawberry, blackberry, lettuce, sweet potato, summer savory, peanut, sunflower, oak, timothy, and oats. It is reported by Chittenden (1900) and other writers as occurring also on the following weeds: ragweed, lamb's-quarters, pigweed, Jamestown weed, cocklebur, black, or garden, nightshade, purslane, fleabane, sand bur, and other plants. The writer has found it on mustard and daisy.

Every time that *S. taeniata* has been found on beans in New York, some of its common weed hosts have been near by. Ragweed and lamb's-quarters appear to be its favorite food plants.

DESCRIPTION OF STAGES

The egg

The egg of *Systena taeniata* (Plate LXX, 3) is elliptical, slightly more rounded at one end, is pale yellow n color, and has a roughened surface. Under the high power of the microscope, the egg covering is seen to be divided into a definite pattern of depressed hexagonal areas, with irregular reticulations in the hexagons. Under a lens it appears faintly roughened. Its length is from 0.6 to 0.65 millimeter.

The larva

The larva (Plate LXIX, 8) is described by Forbes (1894) as follows:

Length 5 mm., greatest width about .6 mm. Slender, widening gradually to the 11th segment, thence tapering quite rapidly. General color pale yellow or brownish yellow, paler towards the posterior end. Head yellowish brown, with numerous stiff hairs; jaws darker brown. Antennae three-jointed, pale, short, and thick. The thorax and abdomen are darkest on the dorsum, fading to paler on the margins and ventral surface, and the latter very pale yellowish at the end. The first thoracic segment has two longitudinal curved impressed lines on the dorsum; segments two and three have longitudinal impressed lines on each side near the border, between which is a transverse curved line crossing each segment near its anterior margin, from which two oblique straight lines extend to the posterior margins of the segments. The legs have stout, blunt, spine-like processes on their anterior surfaces, and stiff hairs on the posterior. The abdominal segments are transversely wrinkled on both anterior and posterior margins. The skin is shagreened, and the whole body is supplied with stiff, spine-like hairs of various lengths. The anal segment has a single fleshy proleg. When seen from above this segment rapidly narrows to midway its length, the posterior half forming a rounded, lobe-like projection of about one half the width of the anterior portion of the segment. On the projection are four long, stiff, spine-like hairs and a marginal crown of shorter spine-like processes, each of which ends in a fine, curved, hair-like lash. (Described from two specimens.)

The pupa

The pupa (Plate LXIX, 9) is pale yellow in color until just before the emergence of the adult beetle, when the darker body markings may be seen thru the pupal skin. The end of the body bears two heavy, prominent, slightly incurving spines. The length is about 4 millimeters.

The adult

The adult (Plate LXIX, 11) is described by Blatchley (1910) as follows:

Elongate-oval. Color variable, usually reddish or brownish-yellow, shining; elytra each always with a paler median stripe; under surface and narrow margins of thorax usually piceous; antennae and legs reddish-brown. Thorax one-fourth wider than long, sides feebly rounded, surface finely and sparsely punctured. Elytra distinctly wider than thorax, finely, shallowly and rather densely punctate. Length 3–4.5 mm.

LIFE HISTORY AND HABITS

The egg

Eggs of the pale-striped flea beetle were nearly mature in dissected females on July 15, 1919, and beetles placed in a cage with ragweed and beans on that date had deposited eggs in the soil by July 22. In 1920 no eggs were found in females opened on June 29, but they were present in specimens opened on July 21. In the cages eggs were deposited for some time after August 6; many were deposited about August 25, and some could still be found on September 8. It may be said that in New York the period of oviposition of *Systena taeniata* extends from the last of July until the first part of September.

In 1919, after finding eggs of *S. taeniata* in cages the writer looked for them in the field, and on July 29 a few were discovered around ragweed. On August 5 some were taken near the roots of lamb's-quarters, and later many more were found around this host. Nineteen eggs under observation in the laboratory hatched in an average of 17 days, with a range from 15 to 23 days.

The egg of *S. taeniata* closely resembles that of *S. frontalis*, which is frequently present in the same habitat, and sometimes it is difficult to distinguish the eggs of these two species. However, the eggs of *taeniata* are smaller and are deposited earlier in the season than those of *frontalis*. Few females of *frontalis* were mature when eggs were found in the field on August 5, and, since a dead specimen of *taeniata* was found in the ground near these eggs, there is little doubt of their parentage.

Eggs of *taeniata* are usually scattered in the ground singly, but they may occur in clusters of from two to seven. They may be found from half an inch to three inches deep, and the writer has always found them near the roots of ragweed and lamb's-quarters tho they no doubt occur also near some of the other hosts of the insect.

The larva

Eggs of *Systena taeniata* have hatched in the laboratory from July 25 to September 8. The newly hatched larvae feed below ground on the roots of their weed hosts. A few small larvae, together with eggs of this species, were found on the lateral roots of lamb's-quarters in August, 1919. Larvae of this species have not been found feeding on the roots of beans.

The writer has not succeeded in rearing these larvae, but it is believed that the insect hibernates in the larval stage near the roots of its host plants. On May 25, 1920, larvae of what is believed to be this species were found around ragweed, but when these were taken to the laboratory for rearing, they died. Later, pupae of *S. taeniata* were found in this same place. It seems reasonably certain, then, that the larval stage normally begins between the last of July and the middle of September, and does not end until late May or early June of the following year. This would make a larval period of from nine to eleven months. In 1886 Forbes (1894) found larvae feeding in young corn plants in Illinois on May 17, and again on July 11 and 12. Chittenden (1903) reports finding larvae feeding on the roots of lamb's-quarters and Jamestown weed.

The pupa

Pupae of *Systena taeniata* were found from June 29 to July 12, 1920, around dead ragweed along the edge of a field that had been in beans the previous year. Twenty were discovered about one plant, three inches below the surface, in rather compact soil. Beetles emerged from these pupae between July 13 and July 25. Forbes (1894) reports pupae emerging on May 26 and June 7 from larvae found on May 17. Adults from these pupae emerged by June 17. It would appear, then, that the pupal stage may cover from two to three weeks.

The adult

Pale-striped flea beetles have been taken in the field from the middle of June until the middle of September. In 1920 the first beetle was seen on June 19 and a few were alive in cages on September 10; the maximum number was present on plants about July 20. The ovaries of female beetles opened on June 29 were very immature, but many well-developed eggs were found in insects dissected on July 21.

It has been noticed each year that when *Systena taeniata* becomes scarce on beans, beetles may still be found on ragweed and lamb's-quarters, especially along the edges of fields. On August 19, 1920, *taeniata* was becoming scarce on beans, but it occurred in large numbers on its weed hosts until about September 3.

During the latter part of their adult life, the females go down into the ground around their favorite food plants to deposit their eggs. In searching for eggs, the writer has often found the beetles crawling in the dirt three inches below the surface. One much battered female was found four inches down in the ground, near a ragweed plant, on September 16, 1919, when most of the beetles had disappeared. On September 23, 1919, a beetle with particles of dirt adhering to its legs and its wing covers was found on ragweed. It had apparently been down in the ground, had deposited its eggs, and had come up again to feed.

The parent beetle of *S. taeniata* lives for a relatively long time and the period of oviposition covers a month or more. Beetles have been seen in copulation from June, when the ovaries were still immature, until September, when nearly all the eggs were deposited. Since the period of egg laying may vary so greatly, it seems likely that some beetles which emerge late in the summer and continue to oviposit for a long time may pass the winter in the beetle stage. Chittenden (1903) states that the insect hibernates as an adult, and Gibson (1913) found overwintering beetles in timothy fields in Ontario (Canada) in May. There is therefore good evidence of adult hibernation in some places, but the writer believes that this is rare in New York. Forbes (1905) believes that in Illinois the insect hibernates as a larva, and the writer's observations point to the same conclusion for New York. Chittenden (1900) believes that there may be a second brood at Washington, but the writer believes that in New York there is only one brood.

SEASONAL HISTORY

The parent beetle of *Systena taeniata*, emerging during June and July, deposits eggs in the ground around ragweed, lamb's-quarters, and possibly other hosts, from July to September. These eggs hatch in from two to three weeks, and the larvae hibernate after feeding for some time on the fine roots of their host plants. During June and July of the next year these larvae emerge as pupae, and after two or three weeks the beetles appear. In New York there is only one generation a year.

CONTROL

Clean cultivation is an important factor in the control of *Systena taeniata*. Fence corners and the edges of fields, which are never cultivated and where ragweed and lamb's-quarters flourish, often become centers of infestation. The pupae of *taeniata* have been found in large numbers around these weeds at the side of a field that had been in beans the preceding year. In this field the beetles were first seen near these weeds in the spring, and thruout the summer, when beans were again planted, the insects were more numerous along this border of the field. When the female beetles are mature they seek out these weed hosts as places for oviposition. The careful eradication of these weeds from the side of the fields and from among the bean plants will help greatly in reducing the numbers of the insect. Eggs are often deposited near weeds growing in the field proper, but it is probable that many larvae and pupae are destroyed when the ground is fitted for the following crop. If these weeds are removed from a field and from its environs late in August, when most of the eggs are deposited, the young larvae will be without food and many will die. One grower planted beans in the same field for several succeeding years, and there were always many *taeniata* present on his plants. Early in September, 1919, he pulled out all of the ragweed and lamb's-quarters growing in the field proper, as well as that along the margin, and in 1920 not more

than one-fourth as many flea beetles were present as there had been the year before. The food supply of the young larvae was removed at a critical time, apparently causing many to die of starvation.

The parent beetles are often numerous on ragweed and lamb's-quarters growing among wheat and oat stubble in the fall; and it has been noticed that when beans were planted in these fields the following year, the beetles were often abundant. Beans grown on land that had previously been in clover in which some ragweed had also sprung up, often show as heavy an infestation of *S. taeniata*. If sod land or stubble land of this type is plowed deep in September, when the larvae are small, so as to destroy the larval food supply, it is probable that the infestation of the following spring will be much reduced.

Artificial control measures tested against *S. taeniata* and the red-headed flea beetle, *S. frontalis*, are discussed on page 1009.

FIG. 93. BEAN PLANTS DAMAGED BY THE RED-HEADED FLEA BEETLE

A few beetles may be seen on the plants

THE RED-HEADED FLEA BEETLE

(*Systena frontalis* Fab.)

A rather large, black flea beetle, with a red head, *Systena frontalis* (of the family Chrysomelidae), may be found more or less abundant in bean fields in New York every year. In dry seasons it is often numerous enough to cause considerable damage to the foliage (figs. 93 and 94). This insect has been found at Perry, New York, each year since 1917, and in 1918, when there was little rain, many beans turned yellow as a result of the feeding of this species and the closely related form, *S. taeniata*. Thirty beetles have been counted feeding on the upper surface of the leaves of a single plant. They often congregate on a few plants, seriously damaging them, while other plants are almost free from the pests.

S. frontalis is a common insect in the United States east of the Rocky Mountains, and in parts of Canada. It has been reported as injurious to grapes, cabbage, beets, potatoes, corn, beans, clover, cranberries, gooseberries, mangle-wurzels, and pear leaves. It is known to occur also on

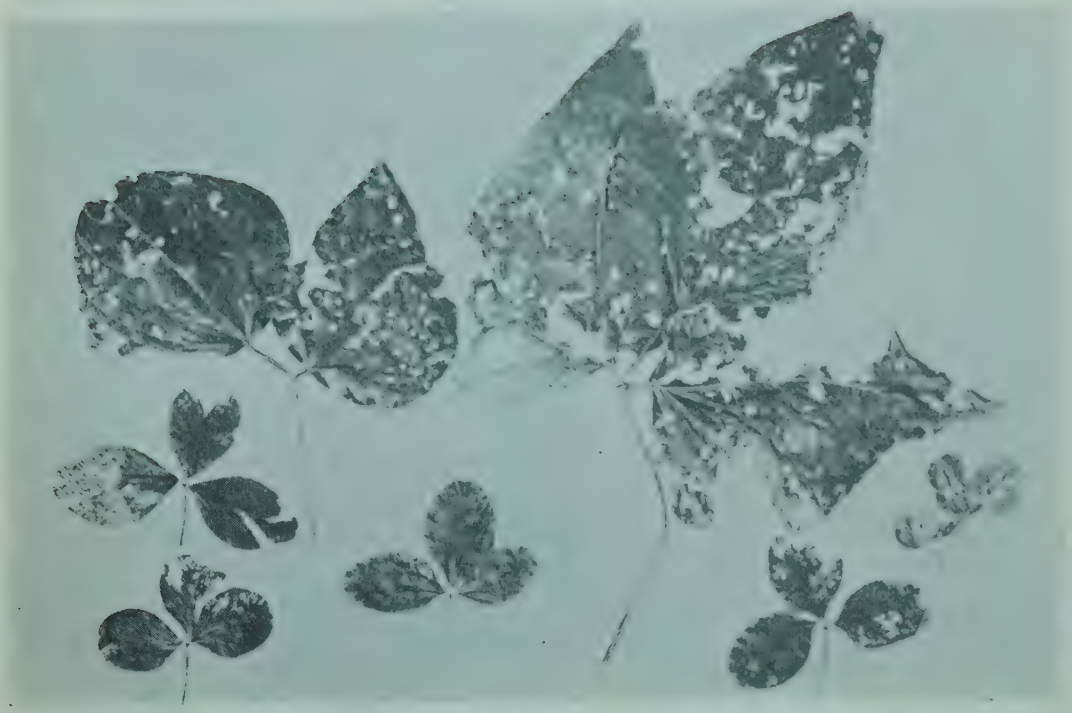

FIG. 94. BEAN AND CLOVER LEAVES INJURED BY THE RED-HEADED FLEA-BEETLE

Japanese honeysuckle, weigela, aster, chrysanthemum, marsh mallow, rose mallow, smartweed, pigweed, lamb's-quarters, and ragweed. In addition to these hosts, the writer has found the species on goldenrod, daisy, broad-leafed plantain (*Plantago major* L.), black bindweed (*Polygonum convolvulus* L.), common burdock (*Arctium minus* Bernh.), heal-all (*Prunella vulgaris* L.), lady's-thumb (*Polygonum Persicaria* L.), wild lettuce (*Lactuca canadensis* L.), and beggar-ticks (*Bidens frondosa* L.).

Where *S. frontalis* has been found in large numbers, some of its weed hosts also have been abundant. Ragweed, lamb's-quarters, and beggar-ticks seem to be the most preferred.

DESCRIPTION OF STAGES

The egg

The egg of *Systena frontalis* is elliptical, slightly more rounded at one end, and is pale yellow in color (Plate LXXI, 6). The surface is roughened. Under high power these roughened areas are seen to be irregular, and they are made by the union of shallow grooves which form the borders of differently shaped polygons. The length is from 0.7 to 0.85 millimeter.

The larva

The larva (Plate LXIX, 7) is dirty white in color, appearing darker where the contents of the alimentary canal show thru the body. The largest diameter is at a point about two-thirds of the distance to the caudal end. The head is pale yellow, with darker markings on the lateral aspect near the lower side. The body is much wrinkled and is covered with many setae. On the caudal end there is a prominent erect tubercle bearing two pairs of prominent spines, and on the apex a tuft of fine hairs. An anal proleg is present. This description is from one specimen, 5.5 millimeters in length and probably nearly mature.

The adult

The adult (Plate LXXI, 8) is described by Blatchley (1910) as follows:

Resembles *hudsonius* very closely. Usually a little broader and less shining, the head reddish or reddish-yellow; antennae and legs mostly pale. Thorax more distinctly and elytra less coarsely punctate. Males in both species with the last ventral segment notched each side, the middle lobe with a deeply impressed triangular median line. Length 3.5–4.5 mm.

LIFE HISTORY AND HABITS

The egg

Immature eggs of *Systena frontalis* were found in dissected females on July 15, 1919. A few mature eggs were found in insects opened on August 5, and many were found in those dissected on August 18. From this time until September 15, eggs were found in beetles that were opened. Eggs deposited in the cages were found after August 6. In 1920 the insects were much later in appearing. The first beetles were taken on July 29, and specimens containing mature eggs were scarce until September 3. Most of the oviposition in the cages occurred early in September. It may be said, then, that the oviposition period varies greatly from year to year, occurring at any time in August or September.

After finding eggs in the laboratory cages, the writer searched for them in the field, and on September 20, 1919, a few were found around ragweed and lady's-thumb After that date, eggs were frequently found on the soil near ragweed, and on September 5 three eggs were located near beggarticks. On September 11, eggs were found near a bean plant in a field where ragweed was growing among the beans, and in the same field, on September 15, one egg was discovered near a plant of lamb's-quarters. As previously stated, the eggs of *S. frontalis* and those of *S. taeniata* are very similar, but the eggs of *frontalis* are larger and are usually deposited later in the season than those of *taeniata*. The eggs of *taeniata* hatch in the fall, while *frontalis* winters in the egg stage. The eggs just mentioned as having been found in the fall of 1919 did not hatch that fall.

Eggs of *frontalis* have been found, in the field, scattered irregularly about the roots of its host plants and from one-half to two inches deep.

Most of the eggs found have been near ragweed and beggar-ticks, tho a few have been found near other hosts.

The eggs of *S. frontalis* that have been under observation have never hatched during the same year in which they were deposited. Eleven eggs deposited on August 24, 1919, hatched between May 20 and 26, 1920. These eggs were kept during the winter on moist dirt in a petri dish in a cool room. Eggs deposited during September, 1920, and kept in a warm office, had not hatched by February 20, 1921. It would seem, therefore, that the egg stage of this insect covers about nine months. Scammell (1917) says: "Egg laying begins in late July, with deposition just below the surface of the ground. Hatching takes place the following May."

The larva and the pupa

Little is known of the larval stage of *Systena frontalis*. Two larvae hatching on May 25, 1920, were reared until June 15. At that time the larger one had reached a length of 5.5 millimeters and was probably nearly full-grown. The writer did not succeed in rearing these larvae thru to pupae. The larval stage is probably passed in feeding on the roots of the insect's weed hosts, but there are no definite data on the larval and pupal parts of the life history. A pupa believed to be that of *frontalis* was found near beggar-ticks in June, 1920, but as it could not be reared the identity is uncertain.

The adult

The red-headed flea beetles have been taken in the field from early in July until the first of October. They are most abundant on beans in August. Beetles have frequently been seen in copulation during August, and in 1920 some were observed as late as September 15.

Blatchley (1910) found the parent beetles of *Systena frontalis* wintering beneath the bark of white maple and in mullein, in Indiana. The writer has not succeeded in keeping the caged beetles alive thru the winter in New York, and, since this insect has not been found in the spring before July, it is doubtful that it hibernates as an adult in this State.

Red-headed flea beetles caged with ragweed or beans will feed actively for a few days and then go into the ground to deposit their eggs. In the field the same condition is found. After feeding on beans they move to ragweed, beggar-ticks, or some other host, where they may be found in numbers until they go into the soil for oviposition.

SEASONAL HISTORY

The parent beetle of *Systena frontalis* comes from the ground in July and August, and, after feeding on its cultivated and weed hosts, enters the ground for oviposition during August and September. The eggs overwinter near the plants, and hatch in May of the following year. The larval

and pupal stages are little known, but the larvae probably feed on the roots of ragweed, beggar-ticks, and other weeds, pupating sometime in June.

CONTROL

It has been pointed out that clean cultivation is an important factor in the control of *Systena taeniata*, and this is equally true for *S. frontalis*. The removal of ragweed, lamb's-quarters, and beggar-ticks from a field

FIG 95. SPRAYING MACHINE USED IN EXPERIMENTS FOR THE CONTROL OF FLEA BEETLES ON BEANS

after the eggs have been deposited in the fall and again before they hatch in the spring, should destroy many of the pests. Many of the insects breed along the edges of fields and in overgrown fence corners, and therefore keeping the weeds cleaned up in these places is a great help in reducing the number of beetles that may emerge.

In the summer of 1919, red-headed flea beetles were numerous in a bean field just across the road from the Perry laboratory, and control experiments were conducted there. On July 18, bean plants were sprayed with arsenate of lead (3 pounds of paste to 50 gallons of water), and twenty-five beetles were placed in a cage over these plants. The same number of

TABLE 12. CONTROL MEASURES TESTED AGAINST SYSTENA FRONTALIS ON BEANS IN 1919

Row	Material, and method of application	Date of application	Length of row examined on July 17 (yards)	Number of *S. frontalis* present on July 17		Length of row examined on July 19 (yards)	Number of beetles present on July 19			
				Total number	Number per yard		*S. frontalis*	*S. taeniata*	Total number	Number per yard
26	Check	.....	35	74	2.11	23	37	6	43	1.89
28	Lime — 1 pound to 2 gallons of water; compressed-air sprayer	July 16	74	14	0.18	74	32	1	33	0.44
29	Check	.....	35	57	1.63	26	48	8	56	2.15
31	Fish-oil soap — ½ pound to 2 gallons of water; compressed-air sprayer	July 16	133	16	0.12	133	59	10	69	0.52
32	Check	.....	37	70	1.89	133	131	14	145	1.09
34	Sulfur — 1 pound to 2 gallons of water; compressed-air sprayer	July 16	88	8	0.09	84	35	3	38	0.45
35	Check	.....	46	67	1.45	26	36	7	43	1.65
37	Arsenate of lead paste (3–50); compressed-air sprayer	July 16	60	5	0.08	55	8	0	8	0.14
38	Check	.....	40	66	1.65	40	23	3	26	0.65
39	Bordeaux (5–5–50), arsenate of lead (3–50); barrel pump on wagon	July 14	90	6	0.06	288	17	1	18	0.06
40	Same as on row 39	July 14	.....	.....	.....	288	21	4	25	0.08
44	Check	.....	79	96	1.21	23	15	4	19	0.82
46	Arsenate of lead paste (3–50); barrel pump on wagon	July 17	.....	.....	.....	84	6	2	8	0.09
47	Same as on row 46	July 17	.....	.....	.....	84	5	1	6	0.07
48	Check	.....	.....	.....	.....	34	24	2	26	0.76
50	Land plaster; dusted on plants	July 18	.....	.....	.....	66	56	15	71	1.07
51	Check	.....	.....	.....	.....	25	31	13	44	1.76
53	Lime; dusted on plants	July 18	.....	.....	.....	54	25	12	37	0.68
55	Check	.....	.....	.....	.....	21	24	13	37	1.76
56	Basic phosphate; dusted on plants	July 18	.....	.....	.....	34	16	6	22	0.64
57	Check	.....	.....	.....	.....	20	21	4	25	1.25
59	Fine ground bone; dusted on plants	July 18	.....	.....	.....	26	9	9	18	0.69
61	Check	.....	.....	.....	.....	28	12	10	22	0.78
62	Superphosphate; dusted on plants	July 18	.....	.....	.....	30	13	15	28	0.93
64	Check	.....	.....	.....	.....	28	18	6	24	0.85
65	Sulfur; dusted on plants	July 18	.....	.....	.....	64	10	1	11	0.17
66	Check	.....	.....	.....	.....	41	17	9	26	0.63
68	Tobacco dust; dusted on plants	July 18	.....	.....	.....	62	15	4	19	0.30

Average of checks, 1.36 beetles per yard

beetles caged over unsprayed beans served as a check. On July 24, eighteen of the twenty-five beetles were alive in the check cage but no live beetles could be found in the cage where arsenate of lead had been applied. Field experiments tested on a larger scale are listed in table 12.

For the experiments recorded in table 12, 94 rows of beans were planted in the field, running from east to west. At least one check row was left alternating with the treated rows. A compressed-air sprayer was used in some of the experiments, but in treating rows 39, 40, 46, and 47, a hand pump on a wagon (fig. 95), with a spray boom feeding twelve nozzles and covering four rows, was used. It was impossible to keep up sufficient pressure to feed all of the nozzles with this pump, and so the outfit would be unfit for practical work unless the boom was attached to a power sprayer or to an efficient traction machine. The three nozzles to a row covered both the upper and lower surfaces of the bean leaves. At this time the plants were still very small, but it is quite possible to spray beans when the vines are more developed. A small hand machine operated by a crank was used in applying the dusts.

Of the materials tested, the bordeaux-arsenate-of-lead spray gave the best results, but arsenate of lead alone was nearly as effective. It is apparent that arsenate of lead has good repellent qualities in addition to its killing power. Sprays of limewater, sulfur, and fish-oil soap also repelled the beetles, tho to a less extent; and several of the fertilizers dusted on the plants kept off some of the insects.

If beans become heavily infested with flea beetles in July, when the plants are small, and if growth is slow because of dry weather, spraying with the bordeaux-arsenate-of-lead mixture or with arsenate of lead alone is beneficial. If suitable machinery is not available for spraying, the plants may be dusted with lime or with a combination of arsenate of lead and lime. In all cases the wild hosts should be removed from fence corners, from the sides of the field, and from the field itself, soon after oviposition is finished in September.

THE GREEN CLOVER WORM
(*Plathypena scabra* Fab.)

During July and until October of 1919, the green clover worm (*Plathypena scabra* (Lepidoptera, Noctuidae) was very common on field beans in New York. The larvae of this snout moth may be found in small numbers on beans in almost any year, but only occasionally is it a serious pest. In 1917 and 1918 the writer found only four larvae of this species on beans.

Among the many hosts of the green clover worm are beans, lima beans, soybeans, peas, cowpeas, vetch, clover, alfalfa, strawberry, blackberry, tickweed, ragweed, smartweed, and wild carrot. The larvae that have been found on field beans in New York apparently belong to the second

generation. As the early-season hosts were not seriously injured, the first generation no doubt developed unnoticed and the pest appeared on beans in midsummer greatly augmented in numbers.

The green clover worm usually hibernates as a moth (fig. 96, B). In the fall the parent insect crawls into strawstacks, into barns, under the bark of

FIG. 96. PLATHYPENA SCABRA AND AGRIOTES MANCUS

A, Pupa of *Plathypena scabra*, × about 3. B, Female moth of *P. scabra*, slightly enlarged. C, Larva of *P. scabra* parasitized by larvae of *Rhyssalus loxoteniae*, enlarged
D, A larva of *Agriotes mancus* entering a diseased bean root, slightly reduced

trees, or to any place where it may be protected from the cold. It is probable that under normal winter conditions a large proportion of these moths die before spring, but the winter of 1918–19 was so mild that the number of insects emerging from hibernation the following spring was far above the average. The mean temperature at Ithaca for the months of December, 1918, and January and February, 1919, averaged 11 degrees higher than

for the corresponding months of 1919-20. In the summer of 1920, which followed an unusually severe winter, the writer could find only one larva of this pest. This was a parasitized specimen (fig. 96, C) found on June 3 on clover, from which eight specimens of *Rhyssalus loxoteniae* Ashm.[8] were reared. From a larva taken on beans on August 22, 1919, another parasite, *Aleiodes intermedius* Cress.,[8] emerged on September 4

When undisturbed, the larva of *Plathypena scabra* rests quietly on the leaf and is inconspicuous by reason of its pale green color (fig. 97, B); but when the plant is shaken, the larva may drop to the ground and squirm back and forth for some time, or it may remain suspended in mid-air by a fine silken thread. The older larvae are voracious feeders. They eat entirely thru a leaf (fig. 97, A), and sometimes make large holes in the pods (Plate LXX, 5).

The pupa (fig. 96, A) is mahogany

FIG. 97. WORK OF THE GREEN CLOVER WORM

A, Bean leaves injured by feeding of the worm, reduced. B, Larva feeding on a bean leaf, slightly enlarged

[8] Determined by C. F. W. Meusebeck.

brown in color, is about 12 millimeters in length, and bears several hook-like spines on the end. This stage of the insect is usually passed above or below ground in a frail cocoon covered with particles of dirt.

The moths of *P. scabra*, reared from larvae found on beans at Perry in July, emerged in cages from August 25 to October 1. Late in September there were many moths in the fields around the piles of drying beans. No eggs were deposited by moths in cages before they were killed by cold weather.

The larvae found in a field at any one time vary greatly in size, and some larvae could still be found when moths were seeking hibernating places. On September 9 larvae of all sizes were taken on beans, and more were found on ragweed on October 2. It seems probable that there are normally two broods of this insect in New York, but that in long warm summers there may be a partial third brood.

When the larvae of *P. scabra* appear in such large numbers that they threaten the bean crop, they may be controlled by a spray of arsenate of lead, 2 to 3 pounds of paste to 50 gallons of water. To insure the destruction of all larvae, the under as well as the upper sides of the leaves should be covered. Sherman and Leiby (1920) found that the pest could be controlled when feeding on soybeans by dusting the plants with a combination of 1 part of powdered arsenate of lead to 8 parts of lime. The material must be applied as soon as the insects begin their work. A hand duster, geared to distribute two pounds to the acre, is recommended by these writers.

On wax and string beans it is not always safe to apply a poison to the pods. To kill the insects on plants of this type, a spray of Black-leaf-40 (1 gallon to 750 gallons of water), with the addition of soap (3 pounds to 50 gallons of water), should be used. For small gardens, a mixture of one teaspoonful of Black-leaf-40 and one ounce of laundry soap in one gallon of water has been found effective. As the larva is killed only when thoroly drenched by the spray, it is necessary to cover both the upper and the under sides of the leaves.

THE BEAN WEEVIL

(*Acanthoscelides* [*Bruchus*] *obtectus* Say)

There is no other bean pest as well known and as much discussed in entomological literature as the bean weevil, *Acanthoscelides obtectus* (Coleoptera, Bruchidae) (fig. 98). It is not a field pest in New York, but, since it frequently causes great loss to beans in storage, a brief discussion of it may be justified in this paper.

When beans that have been infested in the field are kept in a warm storeroom, the reproduction of the weevil continues, and generation after generation develops in the stored seed. The same thing may happen when uninfested beans are put in a warm place where the weevils are already

present. This work in stored beans is the only loss occasioned by this insect in New York (Plate LXXI, 3).

In an effort to determine the summer habits of the weevils that emerge from infested seed when it is planted, the writer, on June 18, 1918, placed weevils, and beans containing larvae and pupae of the insect, in a field cage in which small bean plants were growing. On July 2 it was noted that the parent beetles had eaten small pieces from the leaves of the plants; and on August 15 the beans just below the surface of the ground, that had not germinated, were filled with larvae, pupae, and adults of the insect. This condition still prevailed on October 1.

FIG. 98. THE BEAN WEEVIL, ACANTHOSCELIDES OBTECTUS

Bean weevils are not a serious pest under New York conditions, because of the low temperature during the winter. Garman (1917) has shown by experiments that a temperature of 0° F. for twenty-four hours will destroy all stages of this pest. Thus the insects are probably never able to live thru the cold winters in the bean fields. At a temperature of 50° F., feeding and reproduction are so checked that little harm results. A grower in New York who saves his seed from his crop of the preceding year and keeps it in a barn or some other cold place, need have little fear of weevil injury. The same is true where seed is kept in bean warehouses at low temperatures. In warm stores and seedhouses, however, which often have a few weevils present in left-over stock, the continuous multiplication of the pests often results in almost total destruction of the beans.

FIG. 99. THE BLUE-BANDED MILLEPEDE, × $2\frac{1}{2}$

THE BLUE-BANDED MILLEPEDE
(*Julus caeruleocinctus* Wood)

In July, 1917, a bean field near Batavia, New York, showed a heavy infestation of the millepede, or thousand-legged worm, *Julus caeruleocinctus* (of the order Diplopoda) (fig. 99). The soil in this field is sandy, and when observed by the writer it was dried out and crusted, altho only two weeks before it had been very wet. The millepedes were feeding on the plant parts below ground and had eaten the main roots to such an extent that some of the plants were almost severed from them (fig. 100, C). Nearly every plant

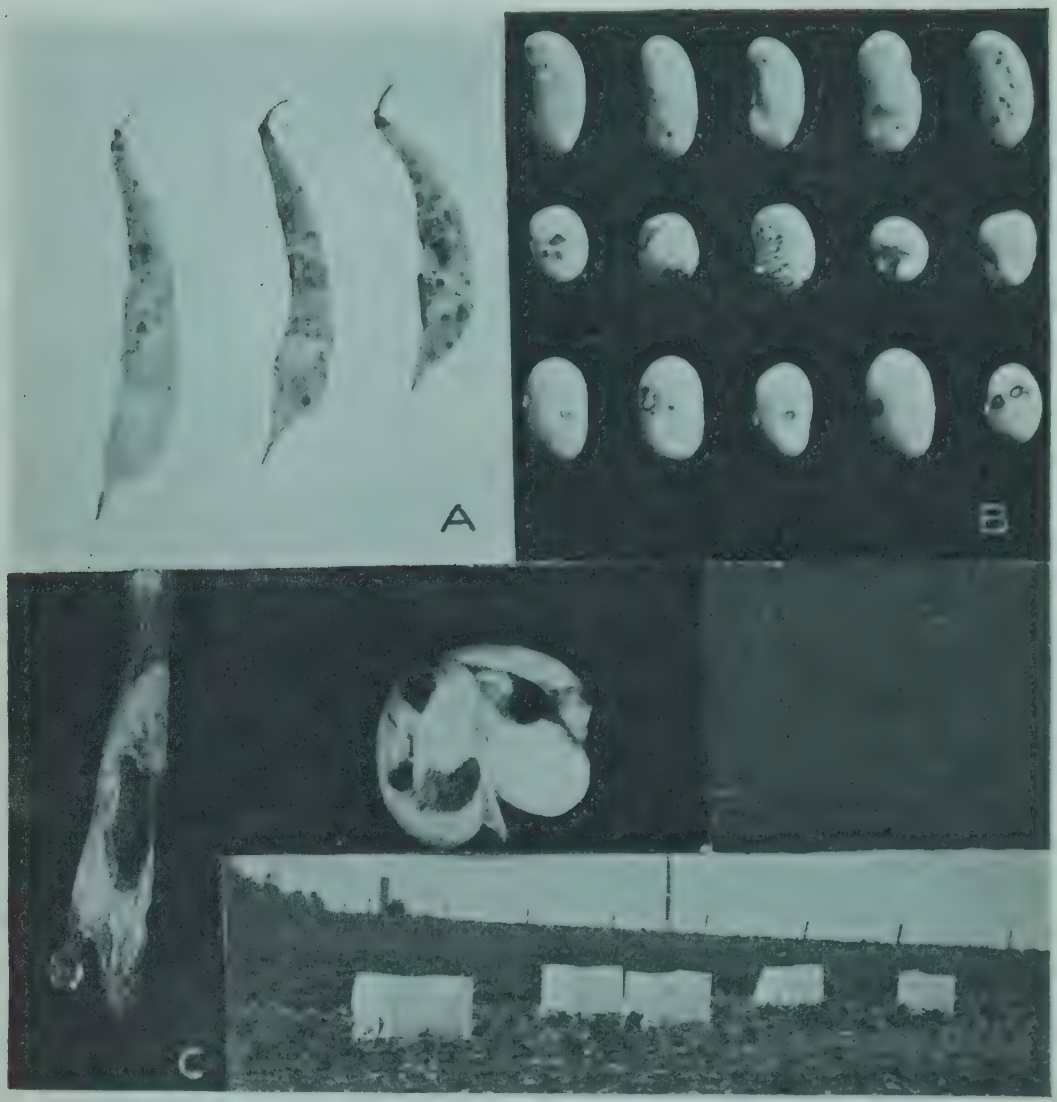

Fig. 100. SOME INJURIES TO BEANS

A, Bean pods punctured many times by *Adelphocorus rapidus*, reduced. B, Dimpled beans caused by punctures of sucking insects, and (bottom row) by a No. 2 insect pin with which they were pricked while still in the pod. C, Cavities made by the feeding of *Julus caeruleocinctus* on roots of beans. × 2. D, insect cages used in experiments in the transmission of bean blight

had been attacked, and frequently there were from five to ten of the pests around a single seedling. Reports of similar injury to beans were received from Orleans and Allegany counties.

J. caeruleocinctus shows a preference for decaying vegetable matter when this is present, but tender growing plants of fleshy texture may be eaten. In Lintner's early writings, records may be found of injury to geraniums,

melons, radishes, potatoes, and turnips. Lintner cites also an instance of injury to nursery stock which was planted after an infested crop of potatoes. The writer has observed these millepedes feeding beneath the ground on young hop vines before they had become hardened, and they have often been found in decaying roots and vines that had been injured by the hop-vine borer (*Gortyna immanis* Guenée). Millepedes thrive under moist conditions, and their attraction to growing plants is often due to decay started in the tissues by excess moisture.

The blue-banded millepede is said to deposit its small, white, spherical eggs in the spring, in clusters surrounded by particles of dirt and excreta. In midsummer, specimens of all sizes may be found feeding together. Two hundred millepedes were found in one potato by Lintner. The pests often gather and crawl over one another, forming moving balls of animal life. Late one evening in September, 1919, at Perry, hundreds were found crawling on sidewalks, in gutters, and even up the sides of houses. By morning they had nearly all disappeared.

There is no satisfactory control for millepedes under field conditions. A bait of poisoned potato buried in the ground is said to be of use in gardens. Tobacco dust seems to have some repellent effect, and on a small scale spraying the ground with Black-leaf-40, 1 part to 750 parts of water as recommended for control of the hothouse millepede (*Oxidus gracilis* Koch), may be effective.

THE SOLANUM ROOT LOUSE
(*Trifidaphis radicicola* Essig[9])

Each year a few bean plants have been found with their roots serving as hosts for the solanum root louse, *Trifidaphis radicicola* (Homoptera, Aphididae). If the aphides are numerous, the leaves turn yellow and the plants take on a wilted appearance, due to the injury to the lateral roots caused by the feeding of the pest. Infested plants have been found from June 22 to August 22. Only the apterous forms of the insect were seen, and usually there were more immature than fully developed lice present. These aphides are cream-colored, but their powdery covering frequently gives them a white, woolly appearance. An ant, *Solenopsis molesta* Say, is often in attendance.

A bean grower near Castile, New York, informed the writer that in 1915 his entire field was so badly attacked that the crop was ruined. When beans were planted in this field the next year they were again infested and had to be dragged up. Lice of this species have also been found in small numbers near Batavia, in Genesee County.

T. radicicola is reported from California by Essig (1909 and 1913) as feeding on rough pigweed (*Amaranthus retroflexus*), beet (*Beta vulgaris*), black nightshade (*Solanum nigrum*), and potato (*Solanum tuberosum*).

[9] Determined by Miss E. Patch.

It is probable that the insect may be found on weeds in New York and is injurious to beans only when they are planted after other infested hosts.

THE WHEAT WIREWORM
(*Agriotes mancus* Say)

Larvae of the wheat wireworm, *Agriotes mancus* (Coleoptera, Elateridae), may be found each year feeding in the roots of field beans near Perry, New York (Plate LXX, 4). This is especially noticeable when the plants are already weakened by the dry root-rot caused by *Fusarium martii phaseoli*. The taproot, partly destroyed by the disease, is a place of easy entrance for the larvae (fig. 96, D, page 1012), and when once inside they frequently eat their way upward as far as the first leaves. Several specimens may be found in a single plant, and if the root-rot also is present the plants often have a drooping, wilted appearance. It is usually impossible to absolutely distinguish the injury caused by the insect from that caused by the disease. Rarely have plants with healthy roots been found to contain wireworms.

Larvae of this species have also been found feeding in the roots of lamb's-quarters and of ragweed growing in bean fields. The life history of the insect covers a period of three years (Hyslop, 1916). Adults were taken by sweeping during May and June in 1919.

As far as the writer has observed, serious injury from wireworms has been restricted to single plants, or, at most, to small parts of a field; and their presence may be explained by the practice of planting beans after sod, which is the normal host of the insect.

THE RED SPIDER
(*Tetranychus telarius* L.)

In a summer that is hot and dry, beans may suffer from the red spider, *Tetranychus telarius* (of the order Acarina) (Plate LXXI, 5). In 1918 the plants on the experimental field at Perry were covered with these pests; the leaves turned yellow and the growth was stunted. The total rainfall at Perry during July and August of that year was only 2.37 inches, whereas the normal for these two months is 6.05 inches. In 1919 the red spider was common in some parts of Genesee, Orleans, and Niagara Counties, where again the rainfall was below normal. It may be occasionally found on beans in any year, but when the growth of leaves is luxuriant the slight damage that it causes is easily overlooked. This mite has many native hosts, and fields that have weeds along the edges or between the rows usually show a heavier infestation.

Injury by *T. telarius* may be recognized by many small brown spots on the upper surface of the leaves, where the plant cells are killed. On the under surface of the leaves, small webs may be observed, and the small yellow, green, or red mites may be found crawling or feeding among

the strands of silk. Each brown area seen on a leaf represents the place of feeding of a mite below, and as these marks increase, the leaf becomes spotted, turns a sickly yellow, and in some cases drops. The lower leaves are attacked first, and as these are destroyed, the small creatures climb higher in search of new food.

WHITE GRUBS, OR MAY BEETLES
(*Phyllophaga* sp.)

White grubs, the larvae of May beetles (Coleoptera, Scarabaeidae), tho occasionally found, have not been reported as a serious pest of field beans in western New York during the past four years. In 1917 the beetles were present in very large numbers around electric lights at Perry. The writer had 184 specimens, collected between June 12 and June 25, identified by Mr. Henry Dietrich, who found 137 *Phyllophaga fusca* Froh. males and 38 *fusca* females, and 6 *P. anxia* (*dubia*) Leconte males and 3 *anxia* females. *P. fusca* is believed by Forbes (1916) to pass thru a three-years cycle. In 1920 a few beetles were collected around lights, but this brood was much smaller than the one observed in 1917. In rare cases the writer has found, in digging around a wilted bean plant, that a white grub had cut it off. Several plants of this type were found in 1919, and one beetle (*fusca*), bred from a grub found on July 3, changed to the adult stage on September 1. It would have emerged normally in the spring of 1920.

Injury from white grubs occurs usually when cultivated crops are planted after sod in a year following one in which there was a large emergence of parent beetles. The May beetles, according to Davis (1918), prefer to oviposit in fields of oats, barley, wheat, timothy, or sod, rather than in those where there are good catches of clover and alfalfa or where there are cultivated crops such as corn and beans. In western New York a common rotation is one of wheat, clover, and beans. If, in this New York rotation, the beetles are abundant during the year when a field is in wheat, there may be many small larvae present the next year; but, since the grubs do not seriously damage clover, the crop then growing, they might easily escape notice. As neither clover nor beans are attractive to the beetle for oviposition, it is evident that when this rotation is followed, little damage from the grubs should be experienced in western New York. Serious infestations of the grub occur only when pasture land or a crop of one of the small grains, such as barley, oats, or wheat, is followed the next year by beans.

THE ROSE CHAFER
(*Macrodactylus subspinosus* Fab.)

In the summer of 1917, beans in many parts of New York were damaged by the rose chafer, *Macrodactylus subspinosus* (Coleoptera, Scarabaeidae).

Reports of injury to the bean crop by this insect were received from Fulton, Lewis, Madison, Essex, and Warren Counties. The principal injury results from the active feeding of the long-legged, grayish brown, adult beetles, which have been reported as destroying as much as 40 per cent of the leaves. Injury from this pest in 1917 was reported between June 28 and August 2.

On grapes, a spray of arsenate of lead (4 pounds of paste to 50 gallons of water or bordeaux mixture, with the addition of 2 gallons of cheap molasses) is said to be the most effective method of control. This should control the insect on beans also. The spray must be applied thoroly as soon as the first beetles are seen, and repeated if rains wash off the first application. Every leaf should be covered, and as a new growth develops this also should be coated with the spray.

THE SOUTHERN CORN ROOTWORM
(*Diabrotica duodecimpunctata* Fab.)

The small, yellowish green beetle (Plate LXXI, 7) known in the South as the southern corn rootworm, *Diabrotica duodecimpunctata* (Coleoptera, Chrysomelidae), and sometimes called the twelve-spotted asparagus beetle, is occasionally present in small numbers on beans in New York. In 1917 it was reported to be causing some injury to the leaves. The parent insect is a general feeder and may be found on many cultivated crops as well as on weeds that occur in and around fields and gardens.

In the South the larvae feed underground on corn and cause immense losses by killing the developing bud. The insects have been found attacking the roots of beans in New York, but there have been so few of them present that the damage to this crop has been negligible. The feeding of the parent beetle on the foliage may be controlled by a spray of arsenate of lead, 2 pounds of paste to 50 gallons of water.

THE BEAN LEAF BEETLE
(*Cerotoma trifurcata* Forster)

Each year a few specimens of the bean leaf beetle, *Cerotoma trifurcata* (Coleoptera, Chrysomelidae), have been found on beans in western New York, but they have not been present in sufficient numbers to cause appreciable damage. The parent beetle (Plate LXXI, 9) is about one-third of an inch in length, and is yellowish in color, with a black head and black markings on the wing covers.

The bean leaf beetle has been found on beans from July until the middle of September. It has been noticed also on ragweed and lamb's-quarters growing in bean fields, and on carrot tops near by. Bush clover, hog peanuts, and beggarweed are likewise reported as hosts. At rare intervals the insect appears in parts of this and other States, destroying field and garden beans, soybeans, and cowpeas by feeding on the leaves.

When control measures are necessary, a spray of arsenate of lead, 2 pounds of paste to 50 gallons of water, applied when the beetles first appear, will suffice.

THE APPLE LEAF HOPPER
(*Empoasca mali* LeB.[10])

The apple leaf hopper, *Empoasca mali* (Hemiptera, Cicadellidae (Plate LXXI, 4), has at times been found in small numbers on field beans at Perry, but the insects have not been connected with any deformation of the plant. In some parts of the State, particularly near Lake Ontario, where pea beans are grown, this insect has been more plentiful, and it has seemed probable that bean mosaic, a destructive disease of pea beans, may be transmitted by this pest. This disease, however, which may be recognized by a curling of the leaves and the appearance of mottled light-and-dark areas on the foliage, has been known to occur and spread when leaf hoppers were not present.

Dr. Robert Matheson, working in conjunction with Dr. Donald Reddick, of the Department of Botany at Cornell University, found that he could produce a curling of the leaves of pea bean plants when leaf hoppers transferred from infested beans were caged over healthy plants. These plants later outgrew the curling, however, and mosaic did not develop, and so the experimental evidence would tend to show that the disease is not carried by *E. mali*. Further tests must be made before a definite statement can be given.

GRASSHOPPERS
(*Melanoplus atlantis* Riley, M. *femur-rubrum* DeGeer, and *M. bivittatus* Say)

Bean fields with a border of grass and weeds, or adjoining meadows or pastures, are often attacked by grasshoppers. Nearly every year a few poorly-cared-for fields have shown some injury. Three specimens of grasshoppers have been mainly blamable for the work — *Melanoplus atlantis*, *M. femur-rubrum*, and *M. bivittatus* (Orthoptera, Acrididae). The eggs of the insects have often been found in fence corners or in the sod border of fields, and many newly hatched nymphs have been taken in these places during May and June. The beans near the edges of fields usually suffer the most; in fact, it is not unusual to find the plants of the first few rows riddled by the pests, while the central part of the field is unharmed.

INJURIES TO BEANS IN THE POD, CAUSED BY HEMIPTEROUS INSECTS
(*Adelphocorus rapidus* Say, *Euschistus variolarius* Palisot de Beauvois, *Lygus pratensis* L.)

During the past four years the Cornell University Agricultural Experiment Station has received many samples of beans showing deformations

[10] Determined by E. D. Ball.

which varied from circular depressed areas, each with a dark spot in the center, to ragged holes, with the bean coat badly ruptured (Plate LXXI, 2, and fig. 100, B). The term *dimples* has been applied to these scars.

Since these markings bear a strong resemblance to hemipterous punctures on other plants, specimens of the dusky plant bug, *Adelphocorus rapidus* (fig. 101), one of the commonest mirids in western New York bean fields, were caged over a potted bean plant on August 15, 1918. When examined on September 4, the pods on this plant were misshapen and covered with dark, raised, wart-like areas (fig. 100, A). The seed in these pods showed evidence of dimpling.

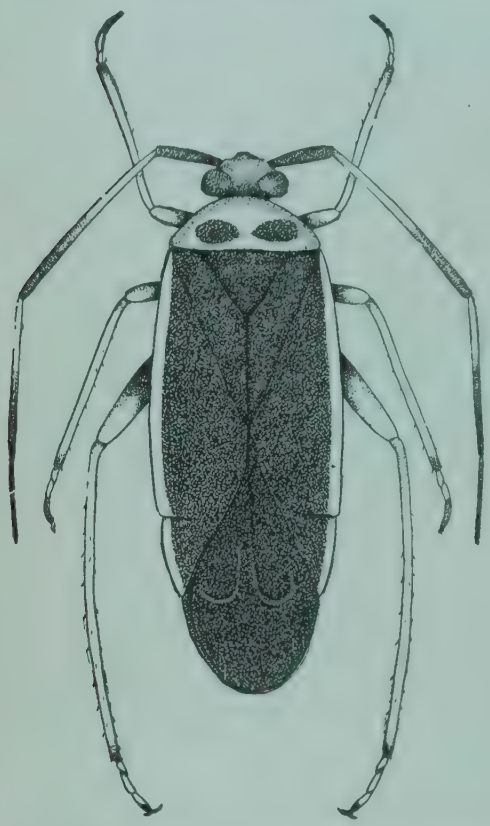

FIG. 101. THE DUSKY PLANT BUG, ADELPHOCORUS RAPIDUS

(Reproduced by courtesy of the Iowa College Agricultural Experiment Station)

In the summer of 1919 an effort was made to verify this observation and to find other insects that might have a share in the work. On August 11 a cage containing *A. rapidus* was placed over two bean plants, the pods of which were still green. When these were examined on August 28, most of the beans were dimpled. One hundred pods picked near the cage contained only one dimpled seed.

The feeding of *A. rapidus* frequently produces such ragged, discolored marks on the bean seed that it would seem that the insect, in addition to removing juices from the bean, possibly secretes a toxin that acts on the bean tissues. The nature of the puncture appears to be influenced by the stage of development of the pod at the time of the attack. The seed is stunted when punctured, and the subsequent growth about the injured part produces the dimple. Beans the pods of which are still green tho nearly mature, tend to suffer the most. In addition to feeding on the pods, the insect attacks also the blossoms, the leaves, and the stalks, but on these no serious deformation seems to result.

It is not always easy to distinguish, by their outward appearance, the pods that contain dimpled beans. The pods may be free from the roughened brown areas and still contain injured beans. Some have been found

on which only a dark green spot on the lighter green of the pod gave evidence of the deformation within.

Other insects that produce pits in beans are the spined tobacco bug (*Euschistus variolarius*, Plate LXXI, 1), of the family Pentatomidae, and the tarnished plant bug (*Lygus pratensis*). Specimens of *Euschistus variolarius* placed with beans on August 19 had produced small pits on them by September 8. Nymphs and adults of *Lygus pratensis* left with a plant for nineteen days also produced small dimples. Similar work of this insect was reported from Michigan some years ago. During late summer both these insects, together with the apple leaf hopper (*Empoasca mali*), have been found in the field with their beaks inserted in the pods. Cage experiments seem to show, however, that the beak of the leaf hopper is too short to penetrate the pod and injure the beans within. In the summer of 1920, these experiments were repeated and the injuries from the insects were of the same kind as had been caused by them the preceding year.

The extent of the damage caused by these pests is not great, but each year there are a few beans of this kind in the product of almost all fields and gardens. Injury is especially noticeable in places where ragweed and lamb's-quarters are allowed to grow. The most disfigured of the field beans are discarded, with the diseased and immature seed, when they are picked and graded in the warehouse.

The Rôle of Insects in the Transmission of Bean Diseases

Bean diseases frequently spread thru a field with great rapidity, and it sometimes appears as tho this spread might be due to, or at least hastened by, the presence of insects. In cooperation with Dr. W. H. Burkholder, of the Department of Plant Pathology at Cornell University, experiments were conducted in the summer of 1918 in an effort to determine what insects were instrumental in the spread of the bacterial blight of beans (caused by *Bacterium phaseoli* E. F. Smith).

On August 22, 1918, eight specimens of each of the commoner insects on bean foliage, including the red-headed flea beetle (*Systena frontalis*), the dusky plant bug (*Adelphocorus rapidus*), the apple leaf hopper (*Empoasca mali*), and the nine-spotted lady bug (*Coccinella novemnotata*), were rubbed in a virulent culture of the blight organism or allowed to crawl for an hour on bean leaves smeared with the culture. The insects were then placed in separate field cages (fig. 100, D, page 1016) on varieties of beans free from blight but susceptible to it. As a check, insects of the same species, collected in the same field but not treated with the pathogene, were placed in similar cages. Blight did not develop in any of the cages.

In 1919 the same species of insects that were used in 1918, and in addition the tarnished plant bug (*Lygus pratensis*), were used in the experiments. The insects were taken from a severely blighted field of red kidney beans, and after being caged for some time with these diseased plants they were

placed in field cages with beans free from the disease. Blight did not appear in any of the cages.

In examining bean seed punctured by *Adelphocorus rapidus*, Dr. Burkholder has found undetermined bacteria present in large numbers. It would seem, therefore, that this common sucking insect might be capable of transmitting the organism that causes bean blight, but most of the evidence thus far obtained is negative.

It is unusual to find *A. rapidus* present in sufficient numbers to be the sole agent in the spread of blight. The writer still feels that the commoner *Lygus pratensis* may sometimes carry the disease as it migrates from plant to plant in search of food, and further experiments should be carried on with *Empoasca mali* before it is safe to say that this species is not partially blamable for the spread of the blight organism. Plant lice have been found but rarely on beans in New York, and never in quantities that would justify placing much blame on them.

Dr. Robert Matheson, working in conjunction with Dr. Donald Reddick, of the Department of Botany at Cornell University, found that he could transfer bean mosaic, the causal organism of which has not been isolated, from one bean plant to another by means of an undetermined plant louse, but that *Empoasca mali*, *Lygus pratensis*, *Systena hudsonius*, *Systena frontalis*, *Epitrix cucumeris*, and *Tetranychus telarius*, seemed unable to transmit the disease.

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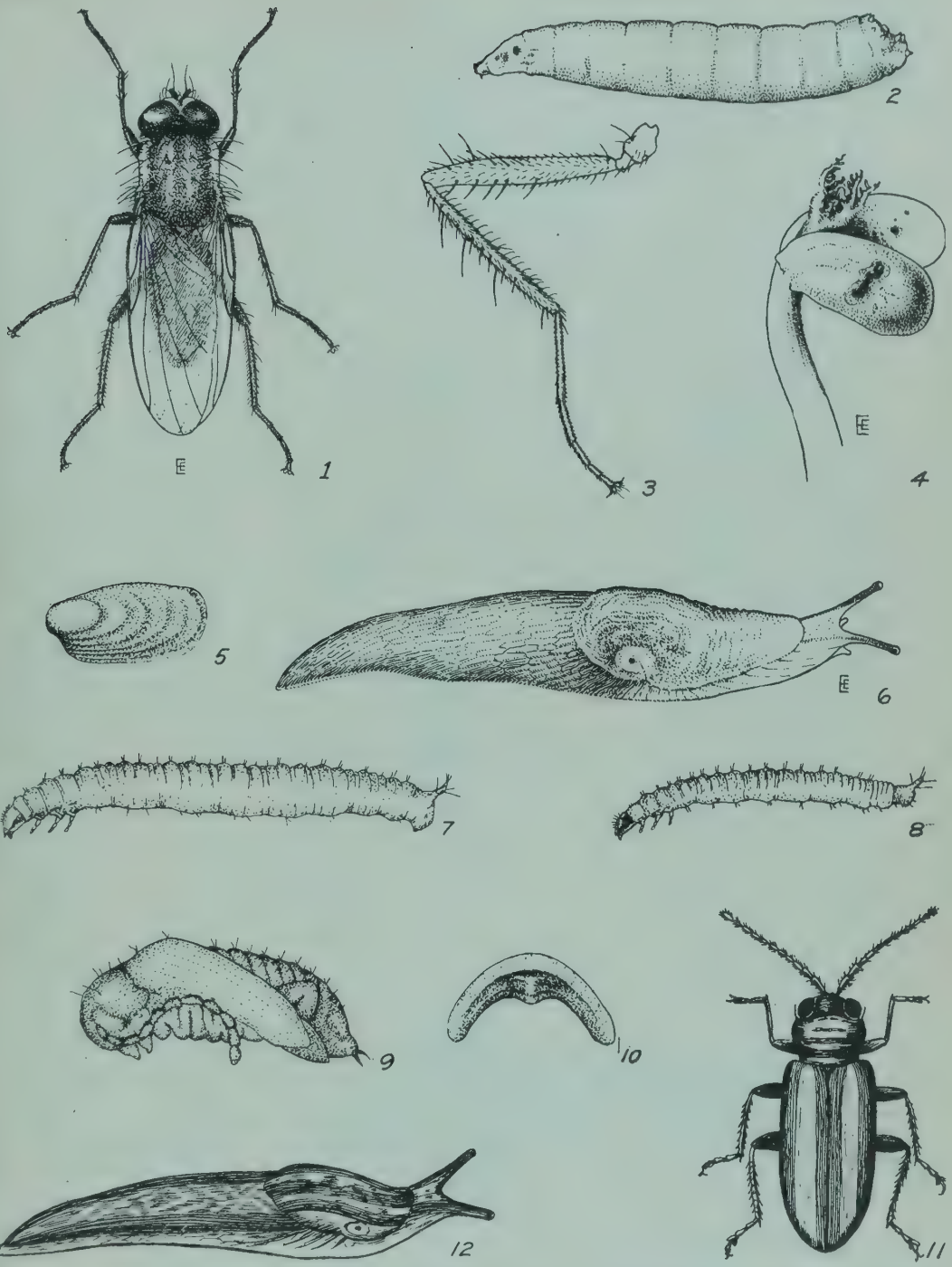
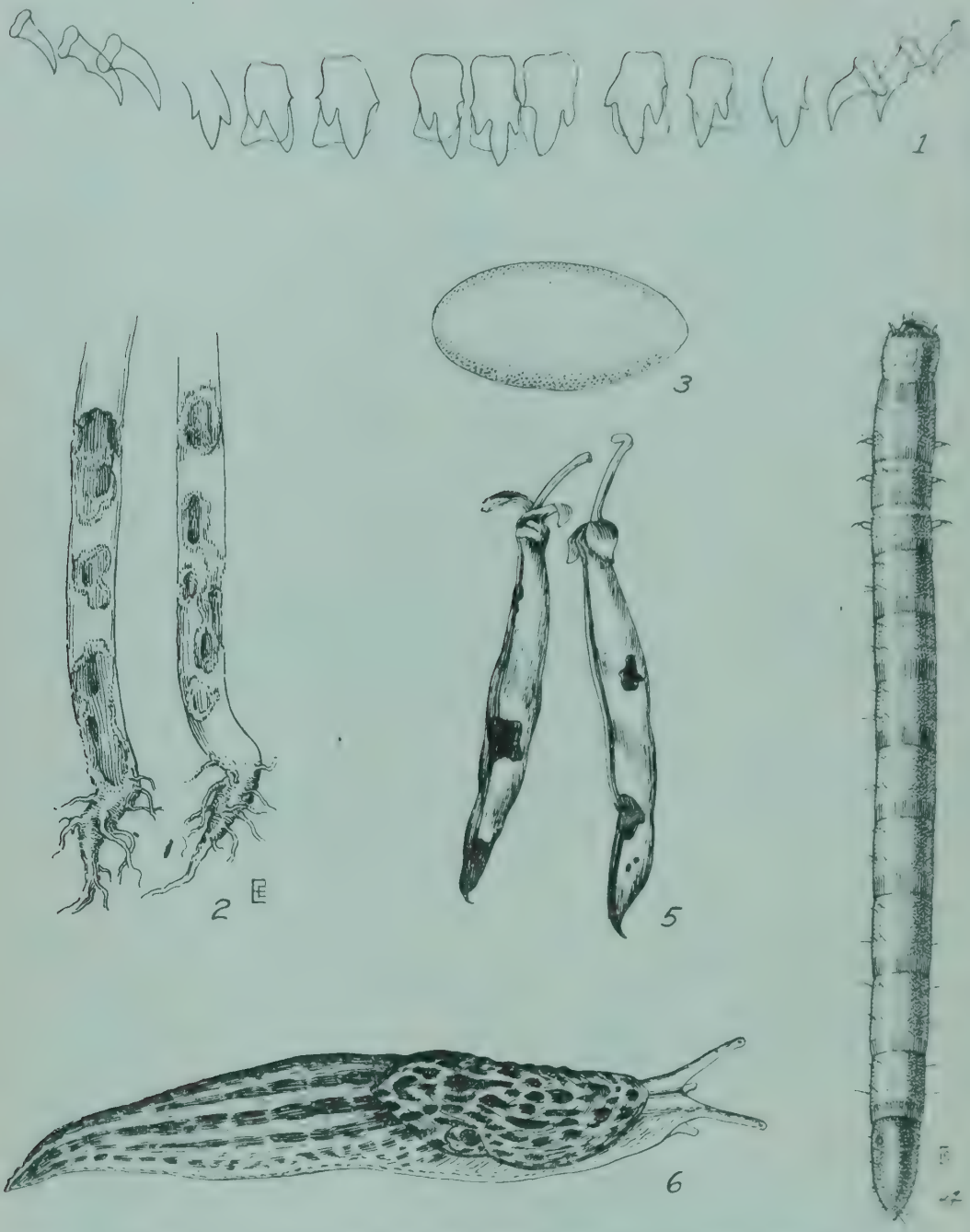


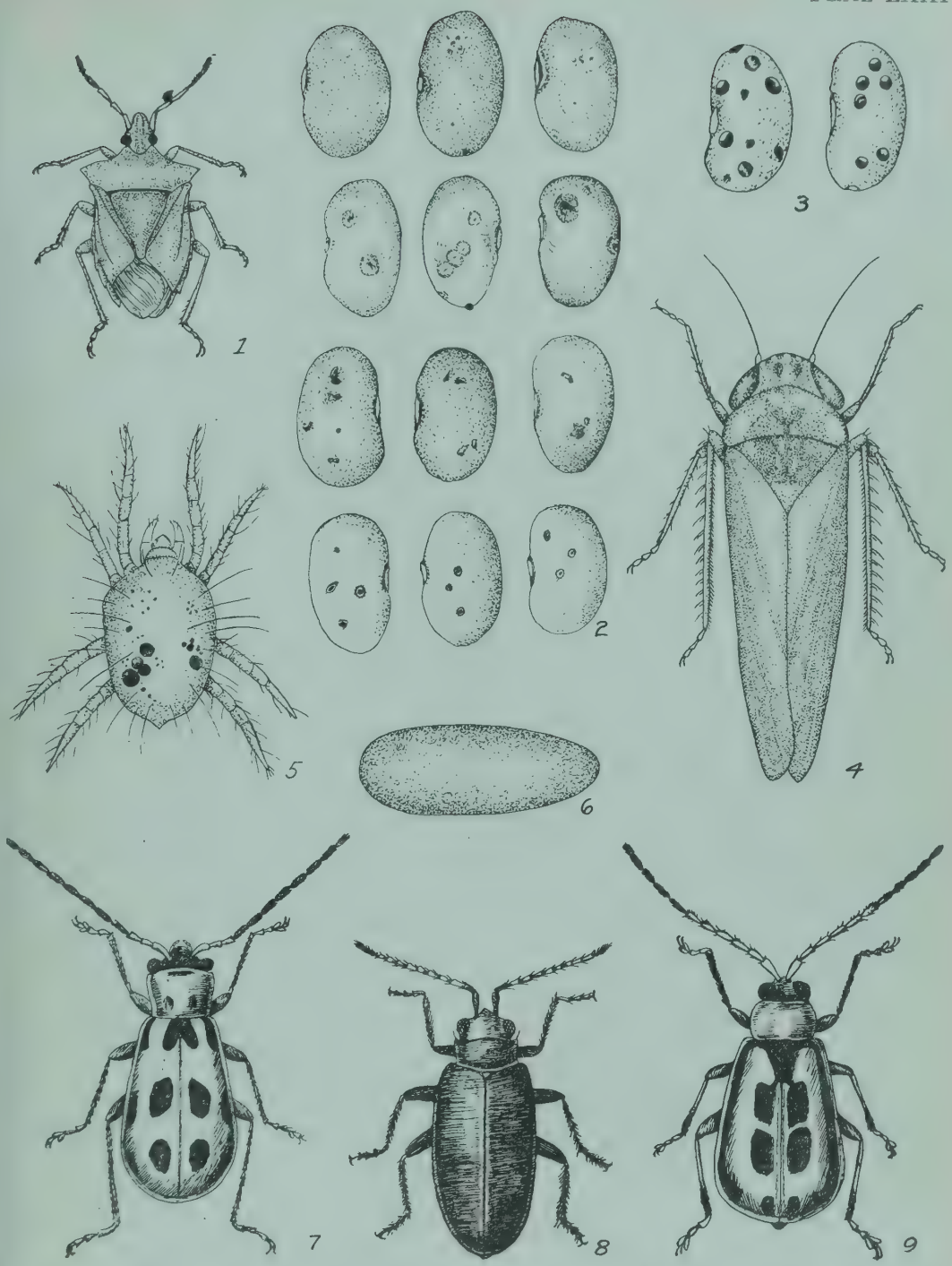
HYLEMYIA CILICRURA, AGRIOLIMAX AGRESTIS, ARION CIRCUMSCRIPTUS, SYSTENA TAENIATA, AND SYSTENA FRONTALIS

Hylemyia cilicrura: 1, Parent fly, with wings in normal overlapping position, × 8. 2, Larva, or maggot, × 8. 3, Third leg of male, showing the row of regular bristles on the tibia, × 18. 4, Injury to the plumule and cotyledons of a bean seedling, caused by the larva of *H. cilicrura*, × 1½
Agriolimax agrestis: 5, The shell. 6, The slug. 10, The jaw of *A. agrestis.* (All redrawn after Taylor)
Arion circumscriptus: 12, A common imported slug, *Arion circumscriptus*, × 2
Systena taeniata: 8, The larva, × 9. 9, The pupa, × 9. 11, The adult beetle, × 8
Systena frontalis: 7, The larva, × 9



STAGES OF VARIOUS SPECIES, AND SOME RESULTS OF THEIR WORK

1, Types of teeth found in the radula of *Agriolimax agrestis* (redrawn after Taylor). 2, Stems of young bean plants showing the result of feeding by *A. agrestis*
3, Egg of *Systena taeniata*, × 48
4, Larva of *Agriotes mancus*, × about 4
5, Feeding holes made by *Plathypena scabra* on small bean pods
6, The spotted garden slug, *Limax maximus*, slightly reduced



STAGES OF VARIOUS SPECIES, AND SOME RESULTS OF THEIR WORK

1, The spined tobacco bug, *Euschistus variolarius*, × 2
2, Beans punctured by sucking insects, causing marks known as *dimples*: top row, dimples caused by *Euschistus variolarius*; second row, by *Adelphocorus rapidus*; third row, by *Lygus pratensis*; bottom row, marks made by a No. 0 insect pin
3, Beans showing the exit holes of the bean weevil, *Acanthoscelides obtectus*
4, The apple leaf hopper, *Empoasca mali*, × 17½
5, The red spider, *Tetranychus telarius*, × 6
6, Egg of *Systena frontalis*, × 40; 8, adult, × 7
7, Parent beetle of *Diabrotica duodecimpunctata*, × 5
9, The bean leaf beetle, *Cerotoma trifurcata*, × 3½

JUNE, 1922

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CONTENTS

	PAGE
The genus Crataegus	1046
Ecological summary	1047
The relation of Crataegus insects to apple, pear, and quince	1050
Biological notes on insects feeding on Crataegus, as observed by the writer from 1917 to 1920	1051
Acarina	1051
Tetranychidae	1051
Eriophyidae	1052
Orthoptera	1054
Acridiidae	1054
Hemiptera	1054
Miridae (Capsidae)	1054
Tingitidae	1056
Cicadellidae (Jassidae)	1061
Membracidae	1063
Aphididae	1063
Coccidae	1065
Thysanoptera	1066
Thrypidae	1066
Coleoptera	1066
Elateridae	1066
Buprestidae	1066
Scarabaeidae	1066
Chrysomelidae	1067
Curculionidae	1068
Lepidoptera	1072
Papilionidae	1072
Saturniidae	1073
Arctiidae	1073
Noctuidae	1073
Notodontidae	1074
Lymantriidae	1075
Lasiocampidae	1075
Geometridae	1076
Sesiidae (Aegeriidae)	1076
Pyralidae	1077
Tortricidae	1077
Yponomeutidae	1078
Elachistidae	1079
Lyonetiidae	1079
Cosmopterygidae	1080
Diptera	1080
Cecidomyiidae (Itonididae)	1080
Trypetidae	1085
Hymenoptera	1086
Tenthredinidae	1086

PAGE

Literature cited 1088
Catalog of insects injurious to Crataegus 1090
Acarina 1090
Orthoptera 1091
Odonata 1091
Hemiptera 1091
Thysanoptera 1100
Coleoptera 1100
Lepidoptera 1108
Diptera 1129
Hymenoptera 1131
Index of genera and species 1133

THE INSECT FAUNA OF THE GENUS CRATAEGUS

THE INSECT FAUNA OF THE GENUS CRATAEGUS

WALTER H. WELLHOUSE

This paper is submitted as a result of three years of study of the insects that feed on the plants belonging to the genus Crataegus. The writer's object at the time when the work was undertaken was primarily to learn, by collecting and rearing, what insects occur on the trees of this genus in central New York. As the interest in the work increased, it was decided to widen the field and make the list more complete by including the insects that other workers have found to be eaters of Crataegus.

There are three older lists of insects feeding on Crataegus which have been helpful in the preparation of the present catalog. Kaltenbach (1872) [1] gives a list of 104 European species, Packard (1890) gives 46 American species, and Felt (1906) gives 28 American species. With the exception of these three lists, the material included in this paper is gathered from widely scattered references and from the writer's observations. Since food-plant indices are very commonly omitted from entomological writings, it is difficult to get a list of all the insects that feed on a plant. Such a list can be obtained only by scanning the pages of a multitude of papers containing biological notes on all orders of insects. Much of that kind of work has been done in the preparation of this catalog, but, since it has not been possible to see all papers that might contain accounts of insects feeding on Crataegus, the writer does not claim that his list is complete.

The catalog contains 382 species, representing 9 orders and 55 families. They are distributed as follows:

Acarina, 10 species:	
Eriophyidae	7
Phyllocoptidae	1
Tetranychidae	2
Orthoptera, 4 species:	
Gryllidae	1
Acridiidae	3
Odonata, 1 species:	
Agrionidae	1
Hemiptera (including Homoptera), 84 species:	
Miridae (Capsidae)	12
Tingitidae	4
Membracidae	4
Cicadellidae (Jassidae)	18
Psyllidae (Chermidae)	7
Aphididae	22
Coccidae	17
Thysanoptera, 1 species:	
Thrypidae	1
Coleoptera, 74 species:	
Elateridae	3
Buprestidae	6
Scarabaeidae	4
Cerambycidae	5
Chrysomelidae	12
Curculionidae	40
Ipidae (Scolytidae)	2
Anthribidae	1
Dermestidae	1
Lepidoptera, 184 species:	
Papilionidae	2
Nymphalidae	2
Pieridae	1
Lycaenidae	3
Sphingidae	3

[1] Dates in parenthesis refer to *Literature Cited*, page 1083.

Lepidoptera (*continued*):	
Saturniidae	3
Arctiidae	3
Noctuidae	27
Notodontidae	6
Lymantriidae	7
Lasiocampidae	10
Geometridae	27
Drepanidae	1
Nolidae	1
Psychidae	1
Limacodidae	1
Cossidae	1
Sesiidae (Aegeriidae)	3
Pyralidae	3
Tortricidae	30
Lepidoptera (*continued*):	
Yponomeutidae	7
Gelechiidae	6
Elachistidae	5
Gracilariidae	12
Glyphipterygidae	2
Nepticulidae	11
Cosmopterygidae	2
Lyonetiidae	4
Diptera, 16 species:	
Cecidomyiidae (Itonididae)	15
Trypetidae	1
Hymenoptera, 8 species:	
Tenthredinidae	7
Chalcididae	1

The catalog includes insects that have been taken on the Crataegus trees in five continents. The number of species reported from each continent is as follows: North America, 213 species; Europe, 203; Asia, 88; Africa, 11; Australia, 8. All but 45 of the North American species are believed to be distinct from those of the Old World. A single Australian species is distinct from those of other continents. The insects recorded from Asia and Africa are found also in Europe.

It will be noticed that the mites, which have similar habits, are included with the insects in this paper.

Some helpful references to entomological notes concerning each species have been included in the catalog, which is intended as an aid to other workers who are investigating the insects of our deciduous fruit trees and related plants.

Grateful acknowledgment is made to Professors Glenn W. Herrick and James G. Needham, of the Department of Entomology at Cornell University, under whose direction the work was done and whose kindly criticisms and suggestions are appreciated; also to Dr. W. T. M. Forbes, Dr. Edith M. Patch, Chas. W. Leng, Dr. P. B. Lawson, Professor Z. P. Metcalf, Dr. H. H. Knight, Professor Carl J. Drake, Dr. E. P. Felt, and Henry Dietrich, who have kindly aided in the determination of species; to Dr. K. M. Wiegand, who has kindly aided in the determination of species of Crataegus; and to Miss Lela G. Gross for able editorial assistance.

THE GENUS CRATAEGUS

Crataegus is the name of a group of trees and shrubs commonly known by their sharp thorns, white flowers (pink or red in a few cultivated varieties) in May, and red or yellowish fruit like minature apples in autumn. It is an ancient Greek name derived from *kratos* (strength), and was applied to the plants of this genus because of the hardness and durability of the wood.

Among the popular names by which the genus is known most commonly are the following: hawthorn, thorn apple, red haw, white thorn, and thorn, in America; hawthorn and may, in England; aubepine, in France (snellier, by French Canadians); Weissdorn, in Germany; spinalba, in Italy. As the name *hawthorn* seems to be the one most commonly used by English-speaking peoples, the writer has used it in this paper to represent all species of Crataegus.

The genus is placed by many botanists in the family Rosaceae. Other botanists have divided the Rosaceae group and formed an apple family, Malaceae, in which Crataegus is included along with Malus, Pyrus, Cydonia, Mespilus, Sorbus, Amelanchier, Aronia, and Eriobotrya.

The determination of species of Crataegus is as great a taxonomic problem to botanists as the determination of the parasitic Hymenoptera is to entomologists. During the first ten years of this century about one thousand species of Crataegus were described in North America. Many of them are now regarded as hybrids and varieties, and a still further reduction of species is in progress. This taxonomic uncertainty makes it impossible in many cases to recognize specific hosts for the insects that feed on the hawthorns.

Crataegus is distributed over most of the temperate parts of the Northern Hemisphere. The genus is not indigenous in the Southern Hemisphere except in America, where it follows the unbroken mountain chain through the Tropics and grows in the Andes Mountains. It is found as far north as Newfoundland, Norway, and Sweden, and extends southward to the Mediterranean borders of Africa and Asia Minor. The European species have been introduced into Australia and other European colonies in the Southern Hemisphere for cultivation.

Most species of hawthorns seem to thrive in any well-drained soil which is not acid and where rainfall is sufficient for the growth of forest trees, while a few species thrive in acid soils also. They are usually long-lived trees, and individuals one hundred years old are not uncommon.

Distribution is effected largely by means of birds and mammals, which eat the ripe fruits and carry the seeds in their digestive tracts to other communities. Within the same community, thickets are commonly formed from the new stems which grow from the roots of a single tree. Wherever the roots become exposed to light, as by washing on hillsides, a new stem may grow and a tree be formed from it.

ECOLOGICAL SUMMARY

The ecological relations of the hawthorns to their insect fauna may be summarized in a general way very briefly. The two basic needs of an insect which it is possible for a host plant to supply are food and shelter. The hawthorns furnish both food and shelter.

They furnish food for nearly all of the insects studied. A few exceptions, such as the snowy tree cricket (*Oecanthus niveus*) and the damsel fly *Lestes viridis*, procure their food elsewhere and use the hawthorn branches merely to shelter their eggs from the weather and their enemies. Every part of the tree furnishes food for some species of insect, as may be seen from the following outline:

Trunk and branches	40 species
A. External feeders (scales, aphids, and others), 19	
B. Internal feeders (borers), 21	
Roots (aphids)	1
Thorns (weevils)	1
Leaves	292
A. External feeders (miscellaneous), 235	
B. Miners (tineids, weevils, sawflies), 37	
C. Gall makers (aphids, mites, cecidomyiids), 20	
Flowers (thrips, maggots, caterpillars, beetles, and others)	12
Fruit (caterpillars, bugs, maggots, grubs)	30

The other basic need of insects which a host plant may supply is shelter. Most of the insects included in this paper are sheltered to some extent by the hawthorn, although the completeness of the shelter varies with the habits of each species of insect. Some are protected only by their position on the surface of the tree. Others are partially sheltered in rolled leaves, bark crevices, and the like. Still others are securely housed within the plant tissues. The degree of shelter secured by those species living externally on the surface of the plant varies so greatly and so gradually that no distinct lines of division can be drawn in so general a statement as this. The more distinct groups of internal feeders (borers, leaf miners, and gall makers) are indicated above and are distinguished from the external feeders, which receive less complete shelter.

The fact that so many species of insects feed at the expense of the hawthorns suggests the idea that these trees are in danger of extinction. Such is not the case, however, for the hawthorns when not weakened by drought or flood are very hardy, long-lived trees. Some indications as to why they so successfully withstand the feeding of the insects may be seen from a study of the following data, which are based on statistics given in the last sections of this paper:

APPROXIMATE FEEDING PERIOD OF HAWTHORN INSECTS

	Species		Species
March	11	August	117
April	54	September	124
May	190	October	80
June	232	November	23
July	131	Time of feeding unknown	58

FOOD PLANTS OF HAWTHORN INSECTS

Food plants restricted to Crataegus	57 species
Food plants including other related or associated groups	325 species

It will be noticed that there is a direct correspondence between the time of feeding of the insects and the time of growth of the trees. The greatest number of species feed during May and June, when the trees make their greatest growth. The number decreases slightly during July and August, at the time when droughts frequently check tree growth, and then it increases slightly in September, at the time when fall rains often cause a new growth. This relationship between the period of growth and the time of feeding seems to be one of Nature's adjustments for maint ining balance.

The fact that a large majority of the insects feed on other host plants also, lessens the danger of destruction of the hawthorns and is another of Nature's provisions for maintaining balance. There are, of course, many other factors that tend to lessen the insect injury to the trees, such as the interrelations of the insects with their parasites and preyers, but so little is known about them that the writer makes no attempt to discuss them.

A host of bees, flies, and beetles visit the blossoms in quest of pollen and nectar. The winter buds in some species of hawthorn become coated with a sticky exudation, which attracts insects emerging in late winter, such as the stone flies and the chironomids. These transient members of the Crataegus fauna have been omitted from consideration in this paper. A list of insects that visit the blossoms is given by Knuth (1908).

In the preparation of the catalog of hawthorn insects it became noticeable that some of the species which have more than one host plant have chosen only closely related hosts, such as the apple, the pear, or the medlar, while many others have chosen their hosts from plants that grow in the same communities regardless of close botanical relationship. A study of these combinations of hosts and the habitats in which they grow has led the writer to believe that the hawthorns are members of at least five different plant communities, which may be described as follows:

1. Open woods. In woodlands where the growth habit of the taller trees permits sunlight to reach the ground so that an undergrowth may develop, such as that in a forest of oak, hickory, and elm, Crataegus is commonly found along with Corylus, Rhamnus, Carpinus, *Prunus spinosa*, and the like.
2. Deforested areas. Where a shrubby growth has sprung up after the destruction of a forest, numerous thorny forms such as Crataegus, Rubus, Berberis, and *Prunus spinosa* are frequently found.
3. Grazing lands. Hillsides or valleys where the soil is uncultivated and cattle are pastured are frequently dotted with Crataegus, Rosa, and crab apple, which because of their thorns can continue to thrive and outgrow the danger of being eaten by the cattle.
4. Stream banks. Just back of the willows and alders on moist alluvial soil beside streams, Crataegus grows to its greatest size and is associated with birch, willow, alder, and poplar.
5. Fence rows. Where shrubs are allowed to grow up along the fences, *Prunus virginiana*, Crataegus, wild plum, and wild cherry are frequently found closely associated.

In each of these five communities insects will be found which feed on the various plants of the community. For example, *Psylla mali* Schmid.

feeds on Crataegus, Malus, Sorbus, Quercus, Ulmus, and Corylus, which may all be found in the open-woods community, as may the host plants of the flat-headed apple-tree borer, *Chrysobothris femorata* Fabr. On the other hand, the leaf beetle, *Cryptocephalus bipunctatus* Linn., feeds near the streams on such plants as Salix, Betula, Crataegus, and Corylus, and *Agrilus rittaticollis* Rand. is found along the fence rows on Crataegus, *Prunus virginiana*, and Amelanchier. No very distinct lines can be drawn between the members of these communities, since many of the plants and insects belong to more than one community.

THE RELATION OF CRATAEGUS INSECTS TO APPLE, PEAR, AND QUINCE

A more complete knowledge of the insects that feed on Crataegus is of considerable importance as an aid in the control of insect pests of the cultivated commercial fruits. It has for many years, since the days of Walsh and Riley, been recognized by entomologists as the original native host plant of a number of important insect pests which now attack the apple, the pear, and the quince in the northeastern section of the United States. In all probability new pests must be expected to attack the cultivated fruits in the future as the population of the country increases, since as a consequence less uncultivated land will remain where the insects may feed undisturbed on their natural hosts.

The main commercial fruits of the United States, such as the apple, the pear, the quince, and the cherry, are natives of the Old World and have been imported by man into America. With them were imported a number of foreign insects, such as the codling moth, the bud moth, and the sinuate pear borer, which continued to feed on them in this country. Many of the pests now destructive to these fruits, however, are native to North America and are not found in the Old World. Before the extensive planting of the imported fruits these insects must have fed on native plants. Among the most numerous of the native plants which are similar to the apple, the pear, and the quince are those of the genus Crataegus, and the members of this genus are widely distributed throughout many of our commercial fruit districts.

A young orchard which is set in the midst of hawthorns may be ruined in a few years by the insects that migrate to it from the surrounding trees. Well-established orchards may suffer from the attacks of new pests whenever there is a failure of the crop of wild haws or a clearing of the land occupied by hawthorns so that their natural guests must seek other hosts.

It is commonly known among entomologists that the apple maggot, *Rhagoletis pomonella*, was originally a hawthorn insect and that after the apple had been cultivated in North America for many years this insect selected the larger, juicier fruit of the apple for its home. It is still found in the haws but is now known as an apple pest.

The apple redbug, *Heterocordylus malinus*, is another hawthorn insect which has adopted the apple. It was formerly believed that the false apple redbug, *Lygidea mendax*, was also originally a hawthorn insect, but the observations of Cushman (1916), as well as those of the writer, indicate that *L. mendax* is a wild-crab insect and does not feed extensively on hawthorns.

The quince curculio, *Conotrachelus crataegi*, is a very common feeder in haws which has occasionally injured quinces seriously and has thus gained its common name. Likewise the lesser apple worm, *Laspeyresia prunivora*, has gained its common name because of occasional migrations from hawthorn to apple.

Baker (1915:10) considers the woolly apple aphis, *Eriosoma lanigera*, to have been originally an elm-Crataegus feeder which has adopted the apple and traveled around the world with it. The woolly aphis is undoubtedly common on hawthorns.

Numerous other native American insects that feed on apple, pear, or quince are included in the catalog of hawthorn feeders beginning on page 1090.

The possibility that foreign hawthorn insects may be imported and become pests in North America should also be considered. When introduced into a new environment away from their natural checks, these may become more important here. Recent examples of this are three small moths imported from Europe — the apple and thorn leaf skeletonizer, *Simaethis pariana*; the hawthorn ermine moth, *Yponomeuta padellus*; and the lesser bud moth, *Recurvaria nanella*. These have attracted the attention of economic entomologists in North America as apple and cherry pests, while in Europe they feed commonly on hawthorns.

Since the catalog of hawthorn insects included in this memoir lists their food plants and the continents where each species occurs, further examples of foreign hawthorn insects that are now in North America may be found there.

BIOLOGICAL NOTES ON INSECTS FEEDING ON CRATAEGUS, AS OBSERVED BY THE WRITER FROM 1917 TO 1920 [2]

ACARINA

Tetranychidae

telarius Linn., *Tetranychus* (Red spider)

The leaves of all species of Crataegus observed showed attack by *Tetranychus telarius*. The European hawthorns, however, seem to be more often severely injured by these mites than the native species. The

[2] The insects are grouped according to order and family, and arranged alphabetically by species within the family.

injury is severest in warm, dry periods. The leaves at first become grayish, due to the presence of a fine white web and the cast skins of the mites attached to them. Later they turn brown and their margins curl toward the surface on which the mites have fed. The adults hibernate among the fallen leaves and a few were found in bark crevices on the trunk in April. The tiny, round, white eggs are laid on the leaves. The mites breed continually on the leaves from June to October.

Eriophyidae

Eriophyes sp. No. 1 (Hawthorn serpentine gall of Jarvis)

The species of Eriophyes here described produces long, green or red, serpentine galls confined to the space between two of the larger veins and extending from the midrib toward the margin of the leaf (fig. 102). The

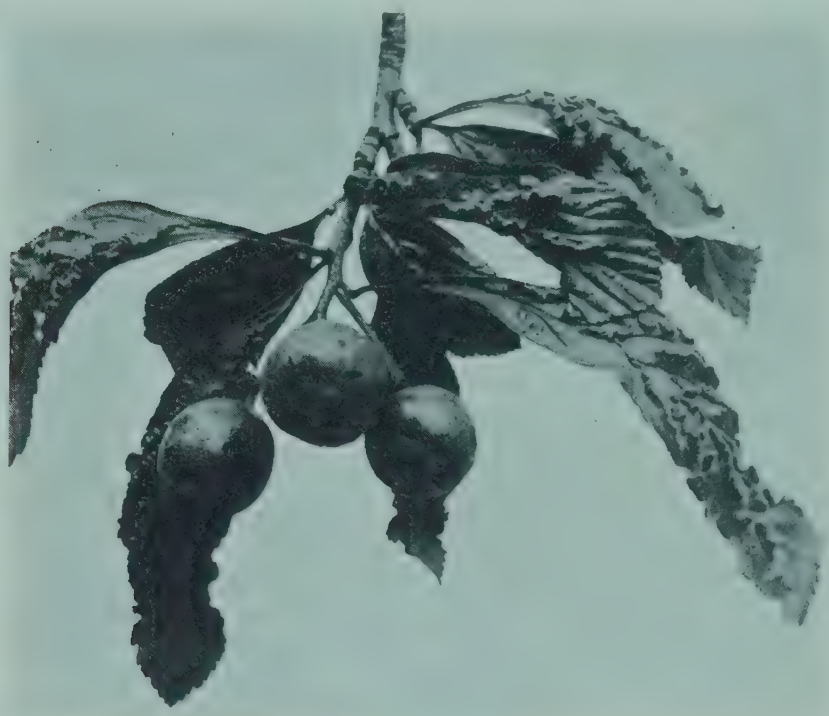


FIG. 102. LEAVES OF CRAETAEGUS PUNCTATA SHOWING SERPENTINE GALLS PRODUCED BY ERIOPHYES SP. NO. 1

gall consists of a wavy projection on the upper side of the leaf and a wavy incision on the lower side. In cross section the leaf appears convoluted, with the galls projecting upward as loops or pockets in which the mites

live (fig. 103). The leaf does not become thickened in these galls. The galls become extremely abundant on some trees, so that almost every leaf is deformed. The mites seem to prefer the shady branches of trees, rather than those in bright sunlight. They become most abundant during August, when the galls are swarming with the microscopic white mites. The galls were found most abundantly on *Crataegus punctata*, but they were found also on *C. pruinosa* and other native hawthorns.

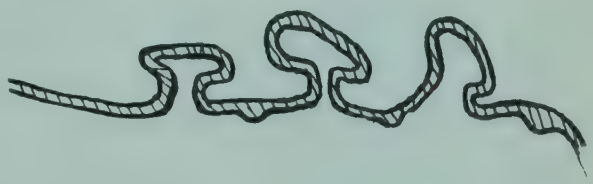


FIG. 103. CROSS SECTION OF A CRATAEGUS LEAF, THROUGH THREE SERPENTINE GALLS

FIG. 104. HAWTHORN MARGINAL GALLS

Eriophyes sp. No. 2 (Hawthorn marginal gall)

Galls very similar to those of *Eriophyes goniothorax* Nal., which are found on hawthorns in Europe, are produced by *Eriophyes* sp. No. 2. The margin of the leaf is curled tightly downward for a distance of two centimeters or more (figs. 104 and 105), and the curled margin is paler green than the rest of the leaf. The mites live within the curl. This gall is not very common about Ithaca, but was found in a few cases on *Crataegus coccinea*.

Eriophyes sp. No. 3 (Thorn leaf pouch gall)

Many small, pale green pouches, standing on the upper side of the leaf and opening beneath the leaf by a small slit, are caused by microscopic white mites which live within the pouches. The galls vary in size and shape, but are generally about two millimeters high and are rounded on top (figs. 106 and 107). They may be found at any place on the leaf except on the larger veins. They are fairly common on *Crataegus punctata* but are not so abundant as the serpentine galls.

FIG. 105. CROSS SECTION THROUGH CURLED EDGE OF LEAF

FIG. 106. THORN LEAF POUCH GALLS

ORTHOPTERA

Acridiidae

atlanis Riley, *Melanoplus*
bivittatus Say, *M.*
femur-rubrum De Geer, *M.*

The common grasshoppers *Melanoplus atlanis*, *M. bivittatus*, and *M. femur-rubrum* sometimes leave their herbaceous host plants to feed on the foliage of the lower branches of hawthorn trees. The older nymphs and adults have been observed feeding in August and September. They feed irregularly on the leaves, sometimes eating the entire leaf and sometimes eating only the apex or one side of it.

HEMIPTERA

Miridae (Capsidae)

communis Knight, *Lygus*

One adult of *Lygus communis* was taken on June 21 and four were taken on August 2, puncturing the leaves of *Crataegus punctata*.

dislocatus Say, *Horcias*

A few adults of *Horcias dislocatus* were found feeding on leaves of *Crataegus punctata* in June. They are black, rather stout, and 6 millimeters long.

malinus Reuter, *Heterocordylus*
(Dark apple redbug)

Nymphs and adults of *Heterocordylus malinus* are very common on native hawthorns, where their red color and rapid running over the branches make them very conspicuous. The young nymphs begin to appear about April 15, when

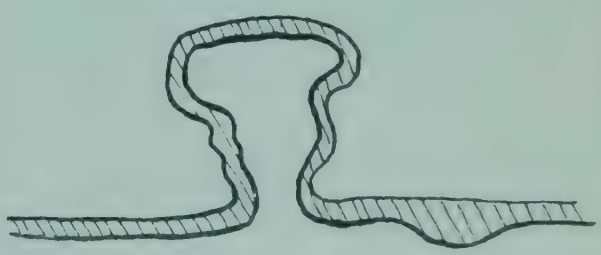


FIG. 107. CROSS SECTION THROUGH A THORN LEAF POUCH GALL

the blossom clusters have just begun to separate and before the blossoms show pink. They puncture the leaves and the tender twigs but do not cause any noticeable injury. After the fruit sets they feed on the fruit also and cause very slight dimples where they puncture it. They become adult in late May and early June, and begin ovipositing in the twigs about June 15. The egg is deposited in a small slit made with the beak at the base of a young twig. Adults were found on the trees until late July.

mendax Reuter, *Lygidea* (Bright apple redbug)

A few nymphs of *Lygidea mendax* were found feeding on the leaves and fruit of Crataegus in late April and in May. They are not so common as *Heterocordylus malinus*. In the warm laboratory the eggs hatched on March 27 on *Crataegus punctata* twigs, but no nymphs were found in the field until the blossoms were opening on April 25. Adults were found from June 2 to August 14. One adult in a breeding cage oviposited on June 19 in a twig of *Crataegus crus-galli*. She chose a year-old twig, drilled a hole through the bark at the base of the twig, and then, turning about, thrust an egg into the cavity.

ornatus VanD., *Orthotylus*

A few adults of *Orthotylus ornatus* were found feeding on the leaves of *Crataegus pruinosa* in June. They are brownish, spotted, slender, and 5.5 millimeters long.

ostryae Knight, *Lygus*

A few adults of *Lygus ostryae* were taken puncturing the leaves of *Crataegus punctata* in late June. They are pale yellowish brown, and are otherwise similar in appearance to the tarnished plant bug.

pellucida Uhl., *Diaphnidia*

The pale green nymphs of *Diaphnidia pellucida* are rather numerous on the foliage of *Crataegus punctata* during late May and early June. They run rapidly over the branches when disturbed, and feed on the leaves and tender twigs. Adults appeared from June 10 to June 15 in rearing cages in the laboratory, and others were found in the field on June 18. They are delicate, slender, pale green, and about 4 millimeters long.

pratensis Linn., *Lygus*

Adults of *Lygus pratensis* which have lived through the winter are sometimes found puncturing the buds of Crataegus in April, as soon as the buds show green, and a few were found puncturing the young fruit in late May.

univittatus Knight, *Lygus*

Adults of *Lygus univittatus* are rather common during late May and June, puncturing the leaves and fruit of native hawthorns. They resemble *L. communis* very closely, but are generally paler.

Tingitidae

bellula Gibson, *Corythucha* (Plates LXXII and LXXIII)

Although the original description of *Corythucha bellula* was published but recently (Gibson, 1918), the species seems to be fairly common where its host plants occur, and it has probably been confused with *C. cydoniae* by earlier observers who must have seen it on the hawthorns. It has been found by Drake in Ohio and by Criddle in Manitoba.

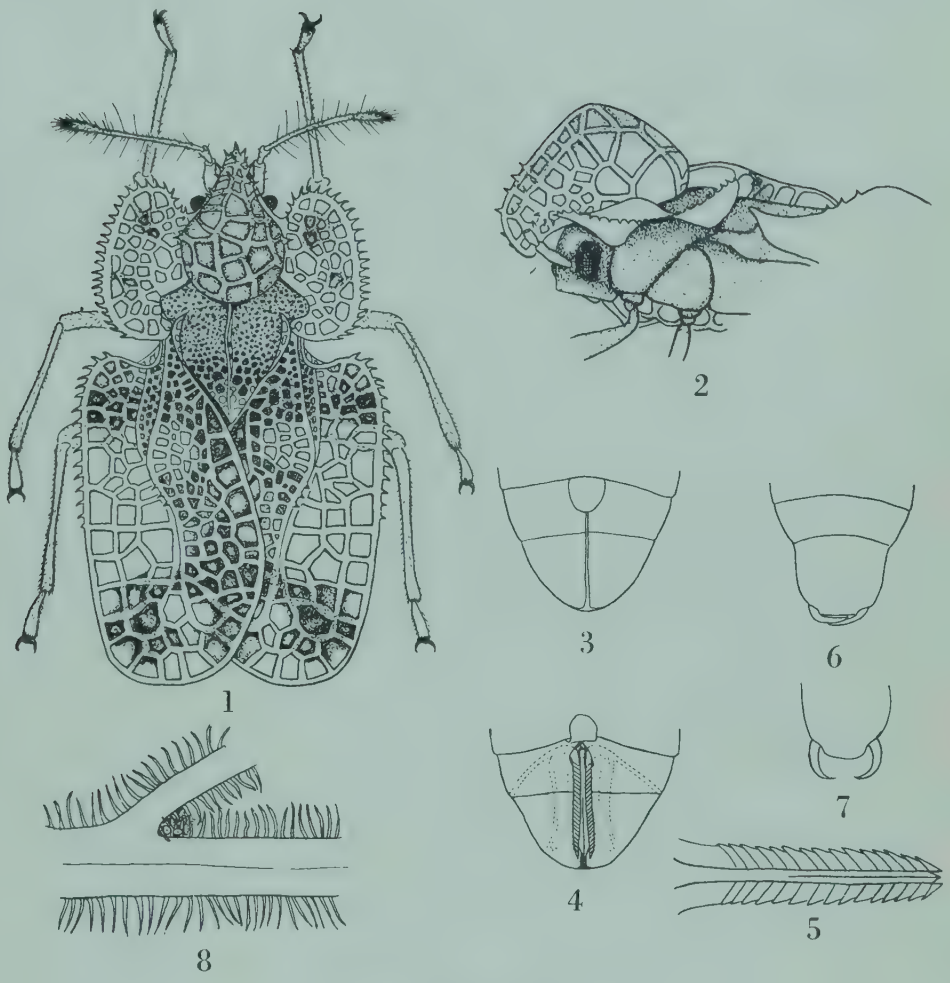
The host plants include those species of Crataegus that have hairy leaf veins, and also *Alnus incana* and *Ribes oxyacanthoides*. The writer has found the insect breeding in abundance on *Crataegus neofluvialis* and to some extent on *C. albicans* and *C. punctata*. The hawthorns with smooth leaves, such as *C. pruinosa*, *C. crus-galli*, and *C. oxyacantha*, even when their branches were intermingled with those of trees that were badly infested, revealed no nymphs nor eggs.

In a large thicket of *C. neofluvialis* trees near the Cornell University campus, the leaves were so discolored by the end of July that they attracted attention several hundred yards away. By the middle of August the leaves were falling, and the branches were bare by September 1. No fruit matured on these trees. A few scattered trees of this species in other directions from the city were also badly infested. Individual trees of *C. albicans* and *C. punctata* showed an occasional branch badly infested and with leaves discolored. The injury is caused by the nymphs and the adults puncturing the under surface of the leaf and sucking the sap, producing at first a mottled effect due to the pale areas around the feeding punctures, while later the leaf turns brown and falls to the ground. Ornamental plantings of Crataegus in parks and gardens are rendered unsightly and weakened by this injury.

There are two generations annually at Ithaca. The first brood hatches in July from eggs laid in late May and in June, and the nymphs become mature in from twenty to twenty-five days. The second-brood eggs are laid in late July and in August, and the adults appear in late August and in September.

The adults of the second brood hibernate among the fallen leaves and in crevices of the bark. Many of them remain on the leaves on which they were feeding before the leaves fell. They appeared the last of May, and during early June were feeding on the new Crataegus leaves. As a rule only one pair of adults was found on a leaf, and they remained feeding and ovipositing on that same leaf for several days. After emergence from the nymphal skin in September, the adults of the second brood continue feeding on the leaves until they fall, in late September or in October.

The egg is subelliptical, with the basal end rounded and the apical end bent slightly to one side and capped with a rather broad cylindrical collar



CORYTHUCHA BELLULA

1, Adult. 2, Lateral view of hood and carina. 3, Tip of abdomen of female, with ovipositor at rest. 4, Same with ovipositor exserted; chitinized parts within body shown by dotted lines. 5, Ovipositor. 6, Tip of abdomen of male, with claspers at rest. 7, Same with claspers exserted. 8, Eggs in position among hairs in axil of leaf veins

surmounted by a low cone with irregular ridges extending from base to apex. From the apex of this cone there arises in some cases a short, blunt prolongation, but often this is absent. The egg is without waxy covering over the chorion, which is smooth, unsculptured, and of a shining dark-brown color but somewhat lighter toward the base. The cap, or cone, is often whitish. The egg, exclusive of the apical prolongation of the cap, is 0.52 millimeter long, and 0.21 millimeter broad at its greatest width.

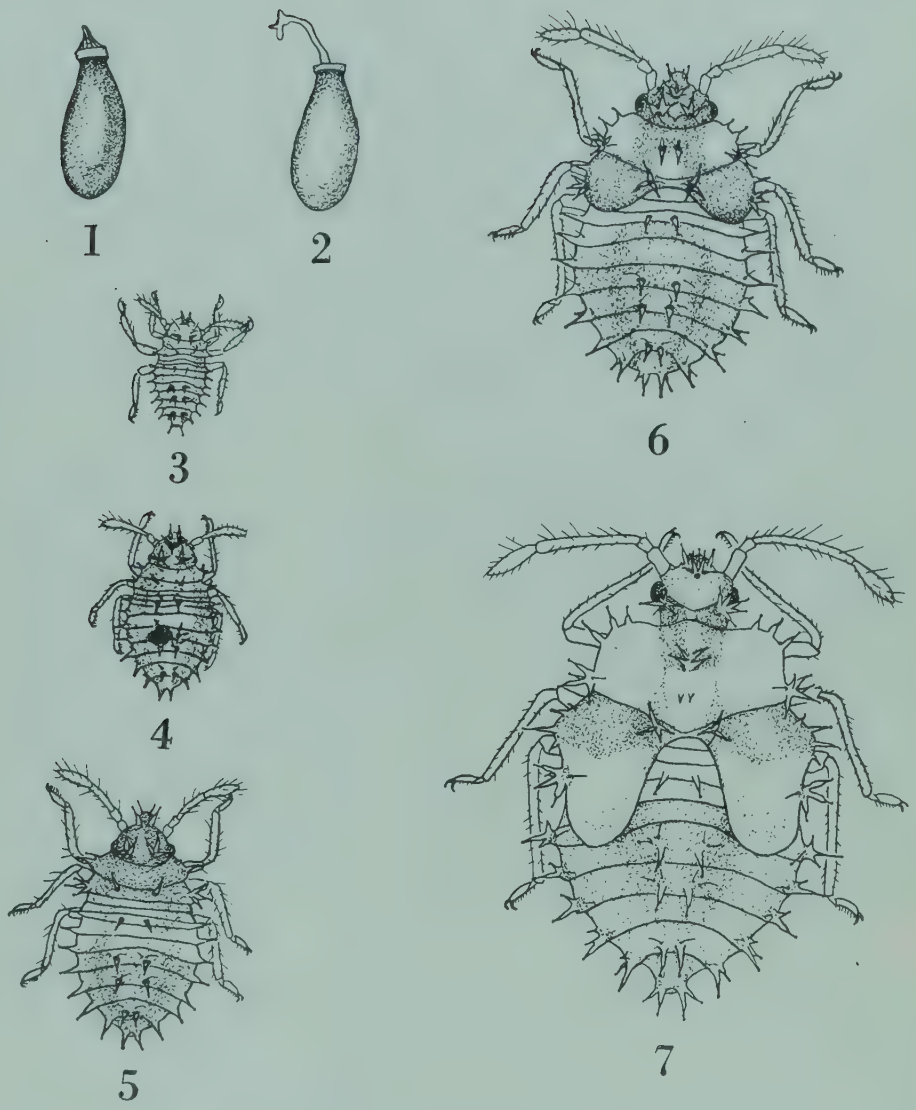
The eggs are laid on the under surface of the leaf, in the axils formed by the midrib and its lateral branches. Although the female has a well-developed, sawlike, four-valved ovipositor, the eggs are not inserted into the leaf tissue. They are placed among the hairs on the veins and are in some cases glued together with an adhesive material. They are generally laid in small groups, some groups containing as many as eighteen or twenty eggs; but occasionally they are laid singly. In counting the number of eggs on one hundred infested leaves the writer found an average of forty-nine eggs to a leaf. Occasionally a leaf had seventy-five or eighty eggs on it. The egg-laying period extends over several weeks, so that eggs, nymphs, and adults may be found at the same time in July and August.

Eggs laid on June 2 hatched on July 9 and 10, while the eggs of the second brood, laid on July 29 and 30, hatched on August 15 and 16. This indicates an incubation period of about thirty-seven days in the cooler temperature of June, and eighteen days in July and August when the average temperature was higher.

The conical egg cap is pushed up by the nymph as it begins to emerge from the egg still inclosed in the embryonic membranous sac. When about halfway out of the eggshell the nymph splits the membranous sac and slips it off over the head, leaving it with the egg cap on the outer end hanging out from the empty eggshell.

After emerging and drying, the nymphs begin to feed at once in colonies near the eggshells. They molt five times, feeding from three to six days between molts, the earlier stages requiring three or four days while the later ones require five or six days. In molting, the cuticula breaks along the median dorsal line from the front of the head to about the second abdominal segment. The insect on emerging is limp, and is almost colorless except for the eye facets which are bright red. The body color soon darkens and the eyes a few hours later become black. During the fifth stage the nymph wanders about more freely over the leaf and in some cases goes to adjoining leaves. Descriptions of the nymphal stages follow.

First stage.— Length 0.5 mm., greatest width 0.15 mm. General shape an elongate ellipse, somewhat broader cephalad than caudad and more elongate than in the later stages. At first almost colorless but soon becoming dark brown. Beak 4-segmented and extending back to sixth abdominal segment. Antenna 3-segmented, the basal two segments being shorter than the third segment; basal segment without spines or hairs, second segment with



YOUNG STAGES OF CORYTHUCHA BELLULA

1, Egg. 2, Egg after hatching. 3, First-stage nymph. 4, Second-stage nymph. 5, Third-stage nymph. 6, Fourth-stage nymph. 7, Fifth-stage nymph

a few short hairs, third segment with numerous long spines and hairs, some with rounded tip and conical base, others with pointed tip. Head with five prominent dorsal tubercles, two slightly separated just above base of beak, each bearing a round-tipped spine; one tubercle back of these on median line bearing two spines; two tubercles near posterior margin, widely separated and each bearing two spines. Pro- and mesothorax having lateral tubercles with a spine on each, and mesothorax having a pair of dorsal tubercles with one spine on each. Metathorax and first abdominal segment without spines. Legs armed with short, pointed hairs and two bent, sharp, terminal claws. Nine abdominal segments visible above, each of these except the first bearing on each lateral margin a tubercle surmounted by a round-tipped spine; two dorsal tubercles on second, fifth, sixth, and eighth abdominal segments, those on second and eighth segments bearing one round-tipped spine each, and those on fifth and sixth segments bearing two spines each; tenth abdominal segment visible from a lateral or ventral view, this segment bearing no spines nor hairs; minute awl-shaped spinules over dorsal surface, especially on large tubercles of fifth and sixth abdominal segments and on thorax. (Plate LXXIII, 3.)

Second stage.— Length 0.68 mm., greatest width 0.27 mm. Body broader in proportion to its length than in first stage; dark brown in color, with numerous minute spinules over dorsal surface, covering it much more completely than in first stage. Additional small spines on both dorsal and lateral tubercles, and the round-tipped spines present before having a slightly longer conical base in this stage. (Plate LXXIII, 4.)

Third stage.— Length 0.82 mm., greatest width 0.44 mm. Antenna with four segments. Round-tipped spines arising from a base longer than the spines, and a few additional small spines on tubercles. Pro- and mesothorax beginning to increase in prominence. (Plate LXXIII, 5.)

Fourth stage.— Length 1.2 mm., greatest width 0.7 mm. Wing pads of mesothorax extending back over metathorax and first abdominal segment at sides. Prothorax more prominent than in earlier stages. Bases of round-tipped spines several times as long as the spines. A few new spines present on lateral margins of pro- and mesothorax and of abdomen. Color dark brown, except in an irregular band across abdomen just caudad of wing pads and on lateral thirds of prothorax, where it is yellowish. Minute spinules covering entire dorsum, light-colored on the yellowish parts and dark on the brown parts; these spinules present also on bases of round-tipped spines. (Plate LXXIII, 6.)

Fifth stage.— Length 1.6 mm., greatest width 0.96 mm. Wing pads now extending back to fourth abdominal segment at sides, and prothorax still more prominent. A few more spines on tubercles; many of the sharp-pointed spines of the earlier stages now round-tipped spines present in the earlier stages on lateral margins of segments covered by wing pads have disappeared. Yellowish parts of prothorax increased in size, and distal part of wing pads yellowish, giving the body the appearance of having two light bands across it. Entire dorsal surface covered with minute spinules as in earlier stages. (Plate LXXIII, 7.)

In all stages of the nymphs the larger spines correspond exactly in position and shape with those so excellently described by Morrill (1903) for the oak lace bug, *Corythucha arcuata*. The only distinguishing characters between the nymphs of the two species which the writer has been able to observe are the size and the prevalence of minute awl-shaped spinules on the dorsal surface. Nymphs of *C. bellula* are smaller, and possess more spinules, than those of *C. arcuata*. The larger spines of both species which are mounted on elongate bases seem to have an eversible sac on the tip which gives them a trumpet shape when it is drawn in and a round tip when it is extended.

The natural enemies of these spiny creatures seem to be few. Only the immature stages of several spiders were seen to prey upon them.

The webs of these spiders sometimes cover the infested leaves of a tree and entangle whole colonies of the lace bugs. The adults that survive the winter are comparatively few, so that the first brood of *C. bellula* does little injury.

Cicadellidae (Jassidae)

clitellarius Say, *Thamnotettix*

The adults of *Thamnotettix clitellarius* are of medium size, 5 millimeters long. They are yellow, with black wings which have a prominent yellow spot. A few specimens were found on June 11.

coccinea Först., *Graphocephala*

The adults of *Graphocephala coccinea* are 8 millimeters long, are slender, with a pointed head, and have the wings striped with alternate red and green. They are found on native hawthorns in July and August, but are not common.

curtisii Fb., *Euscelis*

The adults of *Euscelis curtisii* are small, 4 millimeters long, with many narrow yellow and black stripes. Specimens were found on June 23, but were not common.

fitchi VanD., *Idiocerus* (Black apple leaf hopper)

The adult of *Idiocerus fitchi* is 6 millimeters long, is brown or grayish with oblique white marks, and is found on native hawthorns in July and August. The black nymphs were reared on *Crataegus punctata* leaves from June 14 to July 2. The species winters in the egg stage.

lachrymalis Fb., *Idiocerus*

The adults of *Idiocerus lachrymalis* are 8 millimeters long, and are brownish or grayish mottled, with dark venation. They occur on native hawthorns in June and July. They are not common.

lineatus Linn., *Philaenus*

The adults of *Philaenus lineatus* are 6 millimeters long, brownish yellow, stout with a pointed head, and with a small black spot near the apex on the inner margin of the wing. They are found on native hawthorns from July 1 to July 15, but are not common.

mali LeB., *Empoasca* (Apple leaf hopper)

The adults of *Empoasca mali* are $3\frac{1}{2}$ millimeters long, slender, pale green. They are found rarely on Crataegus in late June.

obliqua Say, *Erythroneura*

The adults of *Erythroneura obliqua* are $2\frac{1}{2}$ millimeters long, with the wings striped red and white. They are very abundant on the leaves of native

hawthorns. They hibernate among the fallen leaves under the trees, and hundreds of them were present under *Crataegus punctata* trees in March, 1919. During warm days in winter they hop about over the leaves. Some individuals have pale pink stripes, and others reddish brown. Adults are found feeding on the trees in June and October.

pallidus Fb., *Idiocerus*

A single adult of *Idiocerus pallidus* was taken on June 23, on *Crataegus punctata*. It was 6 millimeters long, and was similar in size and shape to *I. fitchi* but was almost white.

provancheri VanD., *Idiocerus*

The adults of *Idiocerus provancheri* are $5\frac{1}{2}$ millimeters long, and are brown or blackish with an elongate yellow spot on the base of the inner margin of the wing. They are common on the leaves of native hawthorns during June and July. Nymphs in the rearing cages hatched from eggs in *Crataegus punctata* twigs just as the buds were expanding in April. They became adult in three weeks.

querci Fitch, *Empoa*

The small, whitish leaf hoppers known as *Empoa querci* are very abundant on both native and imported hawthorns. The nymphs may be found on the under side of the leaves in late June and July, and again in September. The adults likewise occur on the under side of the foliage in June, August, and late September or early October. They hibernate among the fallen leaves and become active on warm winter days. They are 3 millimeters long, and are pale yellowish white in color.

seminudus Say, *Eutettix*

The adults of *Eutettix seminudus* are $4\frac{1}{2}$ millimeters long, rather stout, and white with a light brown band across the middle of the wings. They are rather common on *Crataegus punctata* and *C. tomentosa* foliage from mid-July to September.

suturalis Fb., *Idiocerus*

The adults of *Idiocerus suturalis* are $5\frac{1}{2}$ millimeters long, and are pallid except for the black inner margin of the wings. They are found on native Crataegus in June and July, but are rare.

vanduzei Gill., *Eupteryx*

The adults of *Eupteryx vanduzei* are $2\frac{1}{2}$ millimeters long, and are slender with a pointed head. The head, the thorax, and the apical part of the wings are brown, and the central part of the body and of the wings is greenish yellow. One nymph was taken on *Crataegus punctata* foliage, and the adult emerged on August 15. The species is rarely found.

vulgaris Fb., *Lamenia*

The adults of *Lamenia vulgaris* are 4 millimeters long, bluish gray, and rather stout. They are abundant on native hawthorns during the last half of June.

Membracidae

crataegi Fitch, *Glossonotus* (Hawthorn tree hopper)

The adults of *Glossonotus crataegi* are fairly common on the branches of native hawthorns during July and early August.

flavicephala Goding, *Ophiderma*

The adults of *Ophiderma flavicephala* are 8 millimeters long, are brown with a yellowish white stripe on each side and across the rear end of the prothorax, and are without a hump. They are rarely found on the branches of *Crataegus punctata* and *C. tomentosa* during June.

taurina Fitch, *Ceresa*

The adults of *Ceresa taurina* are 8 millimeters long, are pale green, and have the prothorax prolonged into a horn on each side of the head. They are found occasionally on the branches of *Crataegus punctata* and *C. neofluvialis* in late July and August. No nymphs were reared to the adult stage on Crataegus, but several nymphs answering the description of this species as given by Hodgkiss (1910) hatched on April 20 and lived through three instars on *Crataegus punctata* foliage.

Aphididae

corrugatans Sir., *Pemphigus* (Woolly thorn aphis)

A few colonies of the flocculent greenish aphids of the species *Pemphigus corrugatans* were found in early June on *Crataegus punctata*. They live on the under side of the leaves and curl the leaf margins downward.

crataegi Monell, *Macrosiphum*

The apterous females of *Macrosiphum crataegi* may be found from late May until October on the native hawthorns at Ithaca, and during July and August the species may become so abundant as to seriously injure the

FIG. 108. MACROSIPHUM GRATAECI

trees. During the summer of 1919 the writer saw a small *Crataegus pruinosa* tree killed and a very large *C. punctata* tree almost entirely defoliated due to the sucking of sap by myriads of these aphids. They are rather large, yellowish green aphids, with long cornicles, and their most easily recognizable character is the presence of four dark green spots arranged in a rectangle on the dorsal side of the abdomen (fig. 108). The entire life history is passed on Crataegus trees. The black winter eggs are placed on the twigs and the smaller branches. They begin to hatch in May, after the leaves are well opened. The young aphids move to the lower surface of the leaves, and their feeding, as the colony increases, causes the leaves to curl downward.

In late June an alate brood appears and migrates to near-by branches or trees to start new colonies. It is after this brood appears that the species becomes so injurious.

crataegifoliae Fitch, *Aphis*

In early May, 1918, the *Crataegus coccinea* trees at Ithaca began to show the terminal rosettes of curled leaves caused by *Aphis crataegifoliae*. The rosettes turned red, and the aphids within them also were red. The infested branches remained deformed and somewhat stunted throughout the season, although the aphids departed from the trees about May 20 to seek leguminous hosts. No aphids of this species were observed the next year.

FIG. 109. ERIOSOMA LANIGERA ON HAWTHORN

lanigera Hausm., *Eriosoma* (Woolly aphis)

The woolly aphids first become noticeable in early June as small white spots on the tender twigs of Crataegus. In a favorable season such as the summer of 1918, they become very conspicuous and cover entire branches by late summer fig. 109). The writer has not found the roots of Crataegus infested.

pomi De Geer, *Aphis* (Green apple aphis)

During June and July the succulent sprouts of European and native hawthorns are badly infested by green apple aphids. Whenever the weather becomes unfavorable for their enemies they increase rapidly and infest entire trees or hedges, but fair weather checks them again.

prunifoliae Fitch, *Rhopalosiphum* (Apple bud aphis)

The dark green stem mothers of the species *Rhopalosiphum prunifoliae* begin to appear on the buds of native hawthorns as soon as the bud scales have separated enough to show the green leaves within. The colonies increase during April and early May, doing some damage to the young leaves and buds, but before June they migrate from the trees to grasses and are not often found on the trees between early June and late autumn. The winter eggs are laid on hawthorn twigs and buds.

Coccidae

corni Bouché, *Lecanium* (European fruit lecanium)

The species *Lecanium corni* is often very abundant on the lower side of branches of native hawthorns, and occasionally a branch is found to be almost entirely covered with these scales. Lower or inner branches that receive a scanty supply of light appear to be killed by them. The young, flat scales are sometimes very plentiful on the leaves in late summer.

furfura Fitch, *Chionaspis* (Scurfy scale)

The flat, whitish scale known as *Chionaspis furfura* is very common and noticeable on the bark of all Crataegus species which the writer has observed. The small, elongate, white, male scales are often very abundant on the leaves and bark of *Crataegus punctata*. The injury caused by these scales is not noticeable.

perniciosus Comst., *Aspidiotus* (San José scale)

Although the San José scale is fairly common on all species at Ithaca, it does not seem to increase rapidly enough to become injurious. It is more commonly found on the smooth bark of young trees than on old, rough-barked trees.

ulmi Linn., *Lepidosaphes* (Oyster-shell scale)

The oyster-shell scale is common on the bark of native and European hawthorns, and a few badly infested branches have been found. Generally, however, this species seems to be unimportant as a pest of Crataegus.

vitis Linn., *Pulvinaria* (Cottony scale)

The species *Pulvinaria vitis* is occasionally found on the twigs and branches of native hawthorns, but is not very abundant.

THYSANOPTERA

Thrypidae

tritici Fitch, *Euthrips*

Nymphs and adults of *Euthrips tritici* are very common in flowers and flower buds of native hawthorns in April and May. Many flower buds fail to open, and inside of them are found from one to a dozen or more of these thrips. They were exceedingly abundant in the Cornell University arboretum in 1918, and very few hawthorns there bore fruit that year.

COLEOPTERA

Elateridae

dubitans Lec., *Limonius*

The beetles of the species *Limonius dubitans* occasionally are found eating leaves of native hawthorns in late May and early June. On May 31, 1919, one of these click beetles was found on a *Crataegus pruinosa* leaf where it had been feeding, and was attacked by an adult pentatomid, *Apeteticus modestus* Dallas. The latter had its beak inserted into the beetle, which died while being carried to the laboratory.

pubescens Melsh., *Agriotes*

The beetles of *Agriotes pubescens* were eating the leaves of *Crataegus punctata* on May 23. The species is not common.

Melanotus sp.

The beetles of *Melanotus* sp. were eating the leaves of *Crataegus punctata* on June 6 and June 8. The species is not common.

Buprestidae

aerosus Melsh., *Brachys*

The beetles of *Brachys aerosus* were found feeding on *Crataegus punctata* leaves in warm sunlight from May 30 to June 20. There were commonly two or three to a leaf, feeding on the upper surface and cutting small holes through the leaf. As many as fifty of the beetles were found on one tree, while neighboring trees had none. They are from 4 to 5 millimeters long, and are brown and gold in color.

Scarabaeidae

elongata Fabr., *Dichelonycha*

The beetles of *Dichelonycha elongata* were found feeding on *Crataegus punctata* foliage, six being seen on one tree on May 31. A seventh beetle was killed by three adult pentatomids of the species *Apeteticus modestus*, which were feeding on its body.

testacea Kirby, *Dichelonycha*

The beetles of *Dichelonycha testacea* were found on *Crataegus tomentosa* foliage on May 29 and July 1. They cut irregular patches from the edge of the leaf. The species is not common.

Chrysomelidae

borealis Shev., *Dibolia*

The green flea beetles of the species *Dibolia borealis* are $2\frac{1}{2}$ millimeters long. They feed on native hawthorn foliage in May, as soon as it is expanded. They hibernate beneath bark scales on the trunk and the branches, and when warmed in the hand in February they very soon become active.

carinata Germ., *Haltica*

The metallic violet or green flea beetles of the species *Haltica carinata* are 4 millimeters long. They feed on foliage of native hawthorns in June. They are not common.

cucumeris Harris, *Epitrix*

Tiny shining bluish beetles less than 2 millimeters long, of the species *Epitrix cucumeris*, were found feeding on *Crataegus punctata* foliage in June. The species is not common.

helxines Linn., *Crepidodera*

The shining greenish flea beetles of the species *Crepidodera helxines* are 3 millimeters long. They feed on the foliage of native hawthorns and are frequently so numerous as to cause considerable injury. They are found feeding in May, June, July, and August, but are most abundant in late May and in June. The beetles hibernate under bark scales on the trunk and the larger branches, where many of them die from the attack of a white fungous growth before spring.

marginalis Ill., *Systena*

Yellowish brown, slender flea beetles 4 millimeters long, of the species *Systena marginalis*, were found in August and early September eating holes in leaves of native hawthorns. The species is fairly common.

villosula Melsh., *Xanthonia*

The stout brownish or black beetles of the species *Xanthonia villosula* are 4 millimeters long. They were found feeding on the leaves of *Crataegus punctata* from late June to early August. Occasionally they are so abundant as to completely riddle the foliage of a tree with the holes they cut in feeding (Wellhouse, 1919). Feeding punctures are shown in figure 110, on the following page.

FIG. 110. FEEDING PUNCTURES OF XANTHONIA VILLOSULA IN LEAVES OF CRATAEGUS PUNCTATA

Curculionidae

crataegi Walsh, *Conotrachelus* (Quince curculio)

The square-shouldered brown beetles of *Conotrachelus crataegi* were found puncturing the fruit of Crataegus for feeding and oviposition in July and August, 1918, and in late May and June, 1919. The early months of 1919 were much warmer than those of 1918 at Ithaca, and this probably is the cause of the great variation in the time of their appearance. The larvae develop within the haws, feeding on the pulp surrounding the large, stony seeds. A larva commonly eats about one-half of the entire pulp of the fruit before emerging in the autumn, when it leaves the fruit by a large, round, exit hole. It then burrows down two or three inches in the soil and spends the winter as a larva curled in a smooth-walled earthen cell. In June, 1918, the writer found ninety-six larvae in the soil beneath one *Crataegus punctata* tree. Some of them pupated in June and others in July. They are very common on all the native hawthorns.

nebulosus Lec., *Anthonomus* (Hawthorn blossom weevil)

One of the most interesting and injurious of the insects found on the hawthorns is *Anthonomus nebulosus*, a member of a very destructive genus of blossom weevils. Its mode of life resembles in a general way that of the Mexican cotton boll weevil, *A. grandis*, and is almost identical with that of the European apple-blossom weevil, *A. pomorum* (Theobald, 1909: 104–110).

The original description of *A. nebulosus* is to be found in the Proceedings of the American Philosophical Society (Leconte, 1876), and a more complete description is given by Dietz (1891). In the present account it is

sufficient to say that *A. nebulosus* is a brown or grayish oval beetle, from 3.75 to 4.25 millimeters long, generally with a whitish, V-shaped mark on the fore part of the elytra, with a long, slender, curved beak, and the front femur having two teeth on its apical part, one large and the other small (Plate LXXIV, page 1070).

The species has been found in New York, New Jersey, Michigan, Indiana, Missouri, Arkansas, and Louisiana, and therefore it seems probable that it is present wherever its hosts are found east of the Rocky Mountains. Although Dietz considers this species to be more characteristic of the European fauna than of our own, no record can be found of its occurrence in Europe or elsewhere outside of this country.

Its hosts include a number of the larger-flowered species of hawthorns, such as *Crataegus punctata*, *C. brainerdi*, *C. pruinosa*, and *C. mollis*. The smaller-flowered species, such as *C. oxyacantha*, are not selected by the beetles for oviposition, probably because there is not space enough for the full development of the larva within the bud.

The injury caused by the hawthorn blossom weevil is most apparent while the trees are in full bloom. At that time the infested blossoms are brown and remain closed. On badly infested trees fully fifty per cent of the blossoms may be in this condition and the trees present a scorched appearance. As the young fruit begins to set, the infested blossoms commonly fall to the ground, but they may sometimes be seen on the trees even after the beetles have emerged in June.

The beetles come out of hibernation and appear on the branches of the hosts about mid-April, feeding ravenously on the buds, which are showing green. It is not uncommon to see a beetle with feet braced and beak inserted up to the eyes in a bud while it hurriedly eats the tender leaves within. As soon as all the food within reach of the entrance hole is eaten, the beetle seeks another bud on the twig and repeats the process. The puncture in the bud is round, is 0.3 millimeter in diameter, and turns dark as soon as the beak is withdrawn. The presence of the beetles may be detected by these dark round holes in the buds before the egg-laying period arrives. The beetles continue to feed on the buds during suitable weather until the clusters have separated enough for oviposition in the blossoms.

During cool weather the beetles remain inactive, generally in the axils of the twigs with their heads down. A few observations on the relation of temperature to their activities were made, and these indicate that the beetles remain inactive while the temperature is below 50° F. The optimum temperature is from 60° to 70°, and when it is raised to 78° the beetles rush about like mad, attempting to oviposit in every bud. Under most conditions they seem reluctant to fly, but when placed on distasteful food they fly away. They continue their activities on cloudy or rainy days and at night if the temperature is sufficiently high.

ANTHONOMUS NEBULOSUS

1, Feeding punctures of beetles in hawthorn fruit. 2, Egg in blossom bud. 3, Female ovipositing in blossom bud. 4, Flower with petals removed to show full-grown larva in its natural position. 5, Adult beetle. 6, Three flower buds containing larvae, and one normal blossom. 7, Flower with petals removed to show pupa in its natural position

The period between the opening of the blossom clusters and the opening of the blossoms themselves is the time of oviposition, and the length of this period probably influences the amount of injury to a considerable extent. If it is prolonged by cool, cloudy weather, then eggs may be placed in more of the blossoms before they open. In central New York the oviposition period is about May 15.

After selecting a suitable blossom bud, the female makes a hole in the side of the calyx with her beak. Then, turning around, she thrusts the egg into the hole with her ovipositor, and moves to another bud to repeat the process. A clear liquid fills the hole where the egg is thrust in, which soon hardens and seals the opening completely. The act of oviposition requires about ten minutes when the temperature is 68° or 70°, but it requires an hour at 54°.

The egg is pearly white, 0.6 millimeter long, 0.36 millimeter wide, elliptical, generally the same size at both ends but when tucked in tightly between the anthers it may be narrower at one end to conform to the space it fills. It is of almost the same size and color as the anthers and is difficult to distinguish from them. The corium is smooth, unsculptured, and delicate, drying and collapsing when exposed to the air for one hour.

After about a week the young, white, curved, legless larva is found within the bud. It feeds on the anthers, and, as it grows, consumes all the internal parts of the flower but leaves intact the wall of the receptacle and the closed petals which form the roof of its house. The petals become stiff as if they were starched, and do not shrink away as they turn brown. After feeding for a couple of weeks the larva is dirty white, is from 6 to 8 millimeters long, is still legless, has a small brown head, and lies in a curved position. At about this time it molts and changes to a white, free pupa 6 millimeters long, with a dark caudal spine, two dark prominent spines on the apex of the head, and several smaller spines farther back on the head. After pupating during a week or a little longer, the beetle makes a hole in the top or the side of its house with its beak, and emerges.

It begins to feed a few minutes after emergence, choosing for its food the first young thorn or fruit in its pathway as it wanders along the branch. The thorns of the current season's growth seem to be a very attractive food. A hole is drilled near the base of the thorn, and the beetle spends hours with its beak inserted in the hole completely up to its eyes, prying and straining to enlarge the cavity within the thorn. The round hole at the base of a thorn does not heal during the season's growth, and the presence of such holes will indicate at any time of the year the presence of the blossom weevils. The beetles attack the fruit also and make several round holes in a single fruit before seeking another. The holes become brown almost immediately. The writer has never found

the beetles eating leaves or tender twigs, but they sometimes feed on the succulent globular leaf galls of cecidomyiid larvae. They will puncture and feed on young apples in the cages when fresh haws are not to be had, but the writer has found none feeding on apples in the field.

After feeding for a week or ten days the beetles may be found in copulation on the branches, and a week or so later, as warm July weather comes, they disappear from the trees. Those kept in breeding cages remained hidden in fallen curled leaves and hollow twigs on the ground all summer and winter without feeding until the next spring. A search for their hiding places in the field revealed a score of the beetles inclosed in curled, dried leaves on the ground beneath their host trees.

The life cycle may be summarized as follows: The immature stages (egg, larva, and pupa) are completed within the closed blossom in from twenty-seven to thirty-five days, and the remainder of the year is passed in the adult stage. The adults feed on thorns and fruit for two or three weeks after emerging from the blossoms, and then remain quiescent among fallen leaves on the ground until the next spring, when they feed for about a month on the buds before ovipositing. Soon after oviposition the beetles die. In New York the eggs are laid about mid-May and the beetles emerge from the blossoms in June. W. D. Pierce, in a letter to the writer, says the beetles emerge in late March and early April in Louisiana. The time of their development in different latitudes is dependent on the opening of the hawthorn blossoms in those latitudes.

A number of natural enemies of the blossom weevil have been observed. Various birds, especially sparrows, pick open the brown blossoms to eat the larvae and the pupae. Pierce (1912:77) found the weevils to be parasitized by *Catolaccus hunteri* and *Sigalphus* sp. The writer has bred another chalcid, *Habrocytus piercei* Cwfd., from the larva of the weevil, the adult parasites emerging on June 16 and 17.

quadrigibbus Say, *Tachypterus* (Apple curculio)

The four-humped brownish beetles of the species *Tachypterus quadrigibbus* were found occasionally feeding on the fruit of native hawthorns in June. Fruits of *Crataegus punctata* were put into rearing cages on June 25, and from these fruits five adults of this species emerged on July 15 and July 18.

LEPIDOPTERA

Papilionidae

turnus Linn., *Papilio* (Tiger swallowtail)

The green larvae of *Papilio turnus*, with their peculiar eye spots, were found feeding on the foliage of native hawthorns from June 20 to August 2. The species is not very common.

Saturniidae

io Fabr., *Automeris*

The eggs of *Automeris io* are not uncommon on the under side of hawthorn leaves in late June and in July. They are very characteristic and conspicuous. A cluster of eggs may consist of a dozen or more, each large and creamy white with a dark blue dot on the distal end. The larvae feed in colonies on the foliage during July, August, and September. They are at first dark, then green, and are always covered with a mass of dark, stinging spines.

Arctiidae

caryae Harris, *Halisidota* (Hickory tussock moth)

The black-and-white-tufted caterpillars of the species *Halisidota caryae* are fairly common on native hawthorns during August.

tesselaris A. and S., *Halisidota*

The caterpillars of *Halisidota tesselaris* are similar to those of *H. caryae* and are found occasionally on the foliage with them, but are not so common.

textor Harris, *Hyphantria* (Fall webworm)

A single colony of larvae of *Hyphantria textor* was feeding on *Crataegus pruinosa* on July 31, 1918. An egg cluster which was probably of this species hatched on June 19, and the young larvae fed on *C. punctata* leaves for a few days and then died.

Noctuidae

americana Harris, *Acronycta*

The larvae of *Acronycta americana* are green, with an abundant covering of yellowish white hairs and a few long pencils of black hairs. They were found feeding on the leaves of native hawthorns in late June and July. The species is not common.

dactylina Grote, *Acronycta*

The larvae of *Acronycta dactylina* are entirely covered with yellowish white hairs and have three long pencils of black hairs. They were feeding on the foliage of *Crataegus punctata* from August 15 to September. The species is not common.

luteicoma G. and R., *Acronycta*

The larvae of *Acronycta luteicoma* are black, with tufts of white hairs on segments 3 to 6 and tufts of black hairs on the other segments. They were found feeding on *Crataegus punctata* leaves from June 23 to July 22. The species is not common.

occidentalis G. and R., *Acronycta*

The larva of *Acronycta occidentalis* is hairy, with a dark head and dorsal stripes. The remainder of the body is at first whitish but in later stages is reddish. Larvae of this species were feeding on *Crataegus punctata* foliage from August 13 to September. The species is not common.

pyramidoides Guen., *Amphipyra*

The larva of *Amphipyra pyramidoides* is green, with a white dorsal and two yellow lateral stripes, and is found feeding on native hawthorn leaves in May. One larva constructed a silken cocoon among dead leaves on the ground on June 2 and the moth emerged on July 18. The species is not common.

radcliffei Harv., *Acronycta*

The larva of *Acronycta radcliffei* is greenish or black, has a dorsal line of green or brown with faint yellow and red lines, has a hump on segment 12, and is sparsely hairy. It feeds on the leaves of *Crataegus punctata* from June 29 to July 22. The species is not common.

superans Guen., *Acronycta*

The larva of *Acronycta superans* is green, with a black dorsal line widened into a spot on several abdominal segments and with the last segment angularly elevated. There are few hairs on the body. It was feeding on *Crataegus punctata* leaves from June 9 to July 1, and pupated in a silken cocoon among leaves and decayed wood on the ground. The moth emerged on July 23. Only one larva was found.

Notodontidae

concinna A. and S., *Schizura* (Red-humped apple caterpillar)

The brownish, red-humped larvae of *Schizura concinna* feed on leaves of native hawthorns during July, August, and early September. Occasionally they defoliate several branches of a tree, but they are not generally injurious as is *Datana ministra*. They seem to prefer apple to hawthorn. On July 27, 1918, a count was made of the infested trees in several thickets where seedling apples and hawthorns were growing together. Although the hawthorns were much more numerous than the apples, the latter had forty-six infested trees while the former had only three.

manteo Doub., *Heterocampa*

The larva of *Heterocampa manteo* is bright green marked with red. It was found feeding on the foliage of native hawthorns in late June and in July. The species is not very common. One larva taken from a *Crataegus punctata* tree on August 15 continued to feed in the cage until September 2, when it wandered away to find a suitable place for spinning its cocoon.

ministra Dru., *Datana* (Yellow-necked apple caterpillar)

One of the most destructive species to both native and European hawthorns during the past few years has been *Datana ministra*. Very few trees have escaped without at least one colony of these yellow-necked, black-bodied, gray-haired caterpillars feeding on a branch in July and August. Many trees have had an entire branch stripped bare of leaves, and occasionally a whole tree has been defoliated.

The light brown moths appeared and were found ovipositing during June and July. The clusters of white eggs, each cluster containing from 25 to 100, were deposited on the lower side of the leaves and were a common sight in July. The larvae of a colony begin to feed at the tip of a branch and migrate toward its base as they grow, leaving the bare branch behind them. As they become larger they scatter to adjacent branches and feed singly or by twos and threes. They become full-grown and enter the soil in September.

Several observations were made to determine whether the larvae prefer hawthorn to apple. When confined in cages they eat one as readily as the other. In the natural uncultivated areas where hawthorn, apple, and pear grow wild, however, it was noticed that the colonies of larvae were commoner on hawthorn than on the other trees. In one field containing 50 hawthorn, 39 apple, and 17 pear trees, 79 colonies of larvae were counted. Of these colonies 56 were on hawthorn, 15 on apple, and 8 on pear.

Lymantriidae

leucostigma A. and S., *Hemerocampa* (White-marked tussock caterpillar)

The larva of *Hemerocampa leucostigma*, with its bright red head, its red tubercles on segments 6 and 7 of the abdomen, its four white tussocks, and its three long, black pencils of hairs, is a common sight on both native and European hawthorns. It feeds on the foliage during June and July, and the hairy cocoons are common on the branches in winter.

Lasiocampidae

americana Harris, *Epicnaptera*

The large larva of *Epicnaptera americana* is gray with white spots and two red bands above, and orange with a row of lateral diamond-shaped black spots below. It feeds at night on *Crataegus punctata* foliage in July and August. The species is not common.

americana Fabr., *Malacosoma* (Apple tent caterpillar)

During the years 1917 to 1920, only the old egg masses of *Malacosoma americana* were found on the twigs of hawthorns about Ithaca. Only two colonies of larvae were seen on the favorite host, wild cherry, and only one colony on apple.

Geometridae

cognataria Guen., *Lycia*

The larva of *Lycia cognataria* is green and is $4\frac{1}{2}$ centimeters long. It has two pairs of prolegs. On its head are blunt horns, and it bears a prominent red tubercle on the next to the last segment. It feeds on *Crataegus punctata* and *C. pruinosa* foliage in July. It is not a common species.

magnarius Guen., *Ennomos*

A moth of *Ennomos magnarius* emerged from a brown silken cocoon on a twig of *Crataegus pruinosa* on September 30. Eggs were found on a *C. punctata* twig on November 12. The brownish larvae, 5 centimeters long, were found occasionally in May and June.

pometeria Peck, *Alsophila* (Fall cankerworm)

The small greenish or brownish larvae of *Alsophila pometeria* are fairly common on native hawthorns in May.

subsignarius Hüb., *Ennomos*

The white moths of *Ennomos subsignarius* emerged on July 6 and July 18 from pale yellowish pupae which were found tied with silk between the leaves of *Crataegus punctata*. A few of the brown and red larvae were found feeding on the foliage of native hawthorns in May.

tiliaria Harris, *Erranis* (Lime-tree spanworm)

The yellow-and-black-striped larvae of *Erranis tiliaria* are common on native hawthorn foliage in May and June.

titea Cram., *Phigalia*

Two larvae of *Phigalia titea* were found feeding on *Crataegus punctata* leaves on June 2 and June 5.

vernata Peck, *Paleacrita* (Spring cankerworm)

The larvae of *Paleacrita vernata* are common on foliage of native and European hawthorns in May and early June.

Sesiidae (Aegeriidae)

scitula Harris, *Sesia*

A single *Crataegus punctata* tree about eight years old and 5 feet high was killed by the larvae of *Sesia scitula*. The trunk was entirely girdled by four larvae which tunneled beneath the bark two inches above the soil. The sapwood was only slightly indented by their burrows around it. They pupated during June in silken cocoons covered with frass within the burrows, and the moths emerged from July 18 to July 24. In emerg-

ing, the moth pushes through one end of the cocoon, and then sheds the pupal skin while protruding about two-thirds of its length beyond the cocoon. The black, clear-winged moth has a broad and a narrow band of yellow across the abdomen.

Pyralidae

indigenella Zell., *Mineola* (Leaf crumpler)

The cornucopia-like winter cases of *Mineola indigenella*, a leaf crumpler, are easily seen on almost any hawthorn tree during the winter, attached firmly to the twigs and the branches and often with partly eaten leaves attached. The larvae carry the cases with them and feed on the leaves in April and May. They pupate within the same cases attached to twigs in June, and at Ithaca the moths emerge in late June.

Tortricidae

argyrospila Walk., *Archips* (Fruit-tree leaf roller)

The greenish larvae of *Archips argyrospila*, with their black heads and shields, are fairly abundant on the foliage of native hawthorns during May and are found occasionally in June. They tie together a cluster of leaves and feed on a leaf within the cluster. Moths emerged from the larval nests in late June and early July.

chionosema Zell., *Olethreutes*

The pale green larvae of *Olethreutes chionosema* fold the leaves of native hawthorns and feed on the upper surface of the leaves within the fold. Each larva folds a single leaf at a time. They are fairly common on the hawthorns and apple trees about Ithaca during May. The moths fly during June after pupating within the folded leaf. A few moths taken on August 14 and 15 seem to indicate a second brood. The moth (fig. 111) is brownish, with a large white spot on the costal edge of the fore wing, and has a wing expanse of from 15 to 16 millimeters.

FIG. 111. OLETHREUTES CHIONOSEMA

nubeculana Clem., *Ancylis*

The greenish larvae of *Ancylis nubeculana* were found in late summer in rolled leaves of *Crataegus punctata*. They pupated in May and the moths emerged from June 8 to June 18. The species is not very common.

ocellana Fabr., *Tmetocera* (Bud moth)

The brownish larvae of *Tmetocera ocellana* are commonly found in the partly opened leaf buds in April and May, on both native and European hawthorns. The moths emerge from the larval nests in June and early July.

prunivora Walsh, *Laspeyresia* (Lesser apple worm)

The small white caterpillars of *Laspeyresia prunivora* are very common in the fruit of many native hawthorns in late summer. They eat most of the pulp from one side of the fruit, causing the skin to sink in there. The larvae of the second generation sometimes remain in the fruit all winter, living within a mixture of silk and pellets of frass. Others spin silken hibernacula under the bark of the trunk very similar to those of the codling-moth larvae but smaller. They pupate within the hibernacula in the spring and the moths emerge in May and June. In the laboratory they emerged in March. Moths of the first generation were taken in the field from August 15 to August 30.

quadrifasciana Fern , *Eulia*

The yellowish larvae of *Eulia quadrifasciana* tie together with silk the leaves of terminal clusters on *Crataegus punctata* in May. They pupate within the larval nests and the moths emerge in early June. The moth is yellow and orange, with darker oblique bands on the fore wings. The species is not very common.

rosaceana Harris, *Cacoecia* (Oblique-banded leaf roller)

Clusters of leaves tied together by the larvae of *Cacoecia rosaceana* are fairly common on all native hawthorns in May and July. The green-striped larva, with its brown head and shield, is generally found on a single leaf under a slight web, feeding on one side of the leaf only. When full-grown the larva ties a cluster of leaves together to pupate within. Moths emerged from these nests from May 26 to June 30, and a second brood emerged from August 1 to August 15.

Yponomeutidae

oreasella Clem., *Argyresthia*

The small, green, black-headed larva of *Argyresthia oreasella* bores through a terminal leaf bud down into the twig and makes a hole in the side of the twig about $\frac{1}{2}$ inch from the tip, through which the frass is cast out of the burrow. When disturbed the larva runs quickly out of either the hole in the twig or the hole in the bud, to escape. Infested twigs wilt soon after the larva has left the burrow, and then become brown and dry, giving the tree a fire-blighted appearance (fig. 112). Larvae of this species were found in many native hawthorn twigs in May. They leave the

twigs when full-grown, and spin a parchment-like white cocoon surrounded by an open layer of lacework attached to the surface of a leaf. The moths emerged from June 15 to June 30. A few moths taken in the field on August 16 seem to indicate a second brood. The moth is slender, and is white with oblique gold bands on the fore wings while the hind wings are dark gray. Its wing expanse is about 13 millimeters. It has a peculiar habit of standing on its head when at rest on the leaves or the bark.

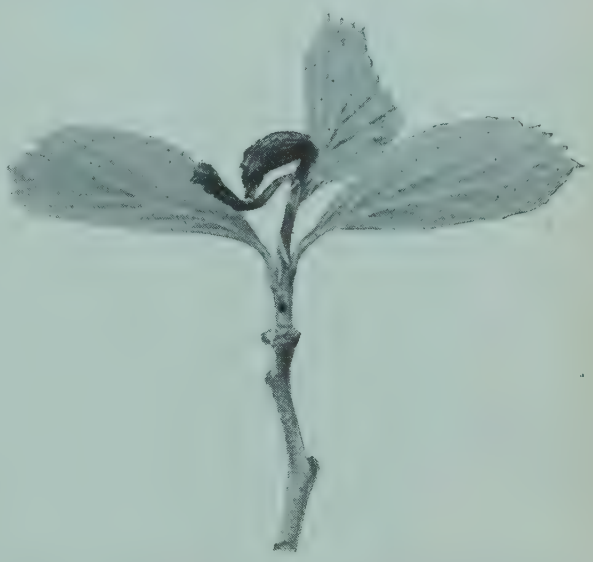


FIG. 112. TERMINAL OF HAWTHORN TWIG DESTROYED BY LARVA OF ARGYRESTHIA OREASELLA

Elachistidae

fletcherella Fern., *Coleophora* (Cigar case-bearer)

The brown, cigar-shaped cases of the larvae of *Coleophora fletcherella* are common on all the hawthorns throughout the growing season. They have been specially abundant and injurious on trees and hedges of *Crataegus oxyacantha*, the European hawthorn, during the years 1918 and 1919. The moths emerged from the cases in late June and July.

malivorella Riley, *Coleophora* (Pistol case-bearer)

The curved cases of the larvae of *Coleophora malivorella* are fairly common on hawthorns but not so abundant as those of *C. fletcherella.*

splendoriferella Clem., *Coptodisca* (Resplendent shield-bearer)

The small, yellowish brown, winter shields of *Coptodisca splendoriferella* are rather commonly found attached to the bark and swinging in the wind on the branches of native hawthorns, and their blotch mines in the leaves are not uncommon.

Lyonetiidae

pomifoliella Clem., *Bucculatrix* (Ribbed-cocoon-maker of apple)

The elongate, white, ribbed cocoons of *Bucculatrix pomifoliella* are common on native hawthorns and are rather noticeable in winter, when the trees are leafless. The moths emerge in late May.

Cosmopterygidae

curvilineella Chamb., *Blastodacna* (Hawthorn fruit miner)

The larvae of *Blastodacna curvilineella* are very commonly found tunneling in the fruit of native hawthorns in late summer. They become full-grown in September and October, when they leave the fruit and burrow into the ends of dead twigs or other decaying wood to hibernate. The hibernation cavity is lined with silk, and in the early spring pupation takes place there. The moths emerge in May and June. They are gray, with two or three indistinct dusky longitudinal short streaks on the wings, and have a wing expanse of 1 centimeter.

The larva is from 9 to 10 millimeters long. In color it is yellowish white, with a brown head and thoracic legs, red spots near the spiracles, more or less blackish among the setae on the dorsum of each segment but especially noticeable on the prothorax and the anal segment, and many patches of black setae arranged as shown in figure 113. It feeds on the pulp of the fruit and leaves many brown pellets of excrement in the burrow behind it. Often one whole side of a fruit is mined out, leaving only the skin to cover it.

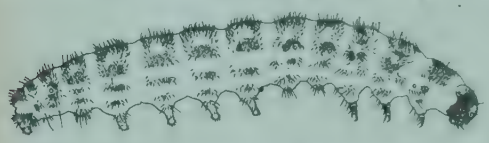


FIG. 113. LARVA OF BLASTODACNA CURVILINEELLA

The moths have been bred from larvae in *Crataegus pruinosa*, *C. neofluvialis*, and *C. macracantha*, and the larvae have been found in a number of other native hawthorns. The moth has been reported by Chambers from Kentucky (1872) and from Canada (1875), and therefore it probably occurs throughout the Eastern States.

A closely related European species, *B. hellerella* Dup., feeds in the fruit of hawthorns and also bores into young apple shoots (page 1116).

DIPTERA

Cecidomyiidae (Itonididae)

absobrina Felt, *Rhizomyia*

crataegifolia Felt, *Lestodiplosis* (Hawthorn fringed-cup gall)

Adults of both *Rhizomyia absobrina* and *Lestodiplosis crataegifolia* have been reared by Dr. Felt from larvae in the galls. The galls are green and cup-shaped, and are covered externally with round-tipped spines 4 or 5 millimeters in diameter and about the same in height (figs. 114 and 115). They occur on the larger veins and petioles of leaves and on the ends of young twigs of *Crataegus pruinosa* and *C. macracantha*. Several galls are commonly found in a group on the same or adjoining leaves. Those on the leaves are on the upper side, but extend through the leaves to form a smooth, semi-globular swelling on the lower side.

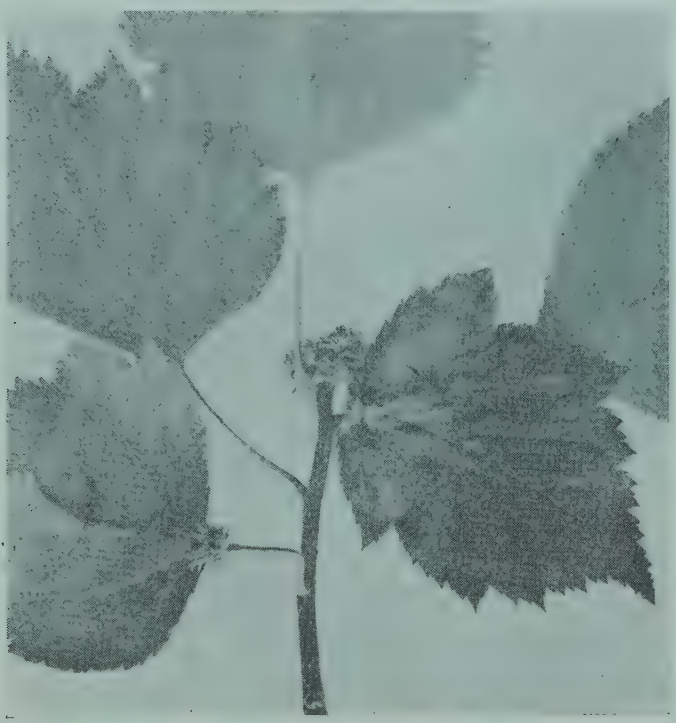


FIG. 114. HAWTHORN FRINGED-CUP GALLS

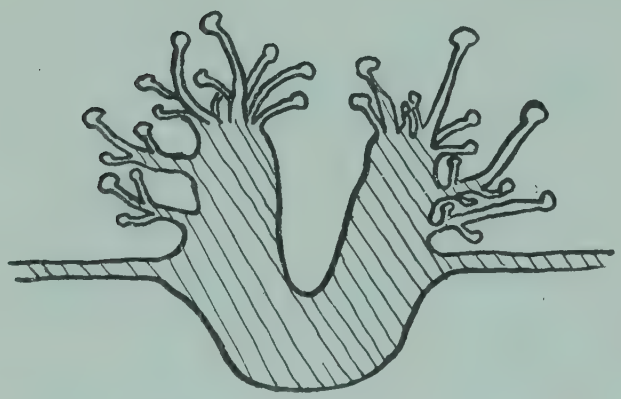


FIG. 115. CROSS SECTION THROUGH A HAWTHORN FRINGED-CUP GALL

FIG. 116. THORN COCKSCOMB GALL

White larvae, 3.5 millimeters long and with a distinct brown breast-bone, were found, one in each gall, in June.

crataegifolia Felt, *Hormomyia* (Thorn cockscomb gall)

Green or red cockscomb-like galls (figs. 116 and 117) produced by *Hormomyia crataegifolia* are found on the upper or the lower side of leaves of *Crataegus pruinosa*, *C. macrosperma*, and *C. coccinea*. They are often in groups on a leaf or a cluster of leaves, and each gall includes a vein. The gall is from 8 to 12 millimeters long and 5 millimeters high, and is open to the outside by a long, narrow slit on the opposite side of the leaf. These galls are found in August.

venae Felt, *Lobopteromyia* (Thorn vein gall)

Round or oval, thick-walled, green galls (figs. 118 and 119) from 5 to 8 millimeters long, produced by *Lobopteromyia venae*, are found on either the upper or the lower surface of leaves of *Crataegus punctata*. The gall opens on the opposite side of the leaf by a narrow slit which extends the entire length of the gall in the direction of the vein. It always includes one of the larger veins. The galls are fairly abundant in June, when several may be found on one leaf and all the leaves in a cluster are deformed.

Cecidomyia sp. (a. 1840 Felt) (Thorn spindle gall)

Red or green, elongate spindle-shaped galls (figs. 120 and 121) 2 millimeters wide and from 5 to 10 millimeters long, produced by *Cecidomyia* sp., are found on either side of the leaves of *Crataegus punctata*. The gall opens by

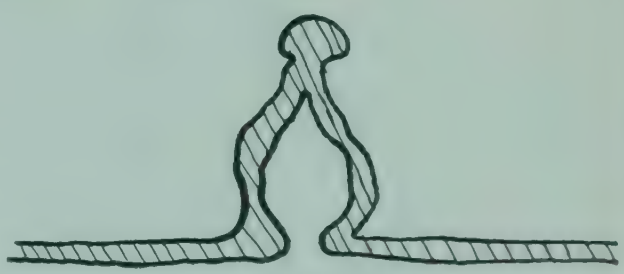


FIG. 117. CROSS SECTION THROUGH A THORN COCKSCOMB GALL

FIG. 118. THORN VEIN GALLS

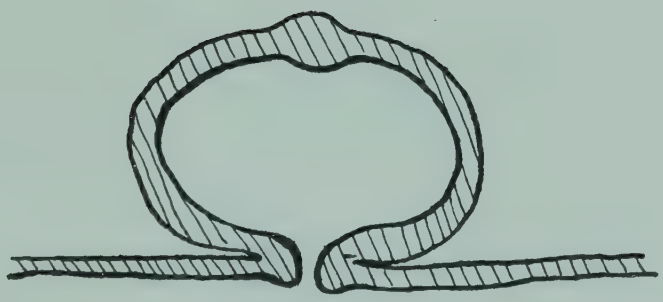


FIG. 119. CROSS SECTION THROUGH A THORN VEIN GALL

FIG. 120. THORN SPINDLE GALLS

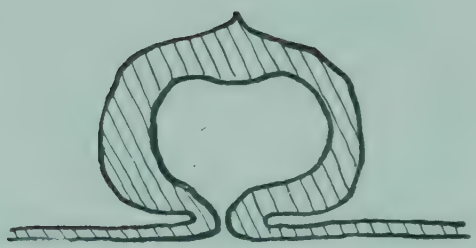


FIG. 121. CROSS SECTION THROUGH A THORN SPINDLE GALL

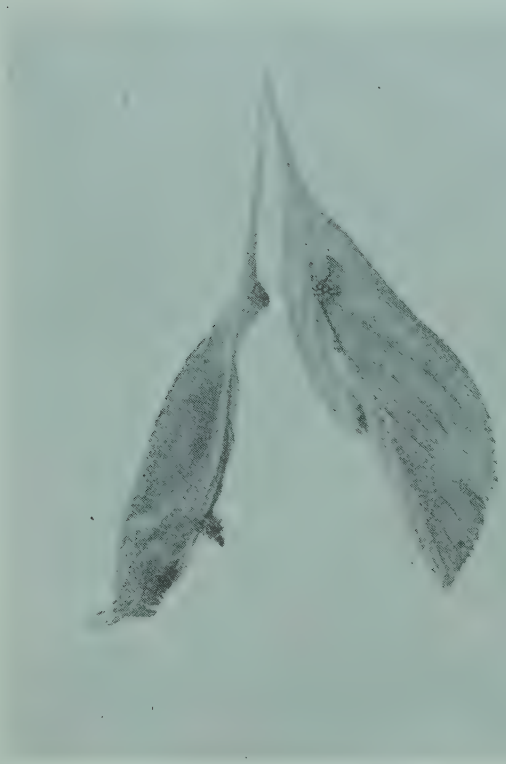


FIG. 122. PINEAPPLE GALLS

a long, narrow slit on the opposite side of the leaf. These galls occur very commonly in groups on the same leaf or on adjoining leaves. A single yellow larva, 1 millimeter long, and slender, is found in each gall in July or August.

Pineapple gall (maker unknown)

Red or green spiny galls, shaped and armored like a pineapple (figs. 122, 123, and 124), 3 millimeters in diameter and 5 millimeters high, are found on the upper side of *Crataegus punctata* leaves in July and August. The pineapple gall is thick and is covered with fleshy spines at the base, but becomes slender, with long, slender spines, toward the apex, which is composed of two flat, leaflike, vertical plates. The gall opens between these two plates. Generally but one gall is found on a leaf and it is commonly on the midvein.

Trypetidae

pomonella Walsh, *Rhagoletis* (Apple maggot)

The maggots of *Rhagoletis pomonella* have been reared and flies obtained from the fruits of *Crataegus punctata*, *C. albicans*, *C. pruinosa*, *C. brainerdi*, and *C. macrosperma*. The species probably lives also in the fruits of other large-fruited hawthorns. No larvae have been found in the small fruits of *C. neofluvialis* and *C. oxyacantha*, although these have been carefully watched. The maggots leave the fruit to enter the ground in autumn, and the flies emerge from the brown puparia in June and July.

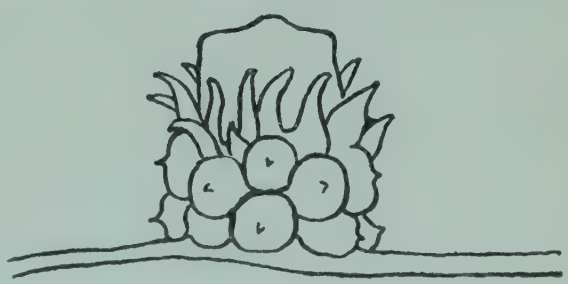


FIG. 123. SIDE VIEW OF PINEAPPLE GALL

All of the flies reared on hawthorns are equal in size to those reared on apple, not small like those reared on the blueberry. Counts were made of the infested and the uninfested fruits from a square yard beneath each of ten trees of the three species first mentioned in the preceding paragraph. The counts showed that from 20 to 25 per cent of the samples taken were infested by the maggots.

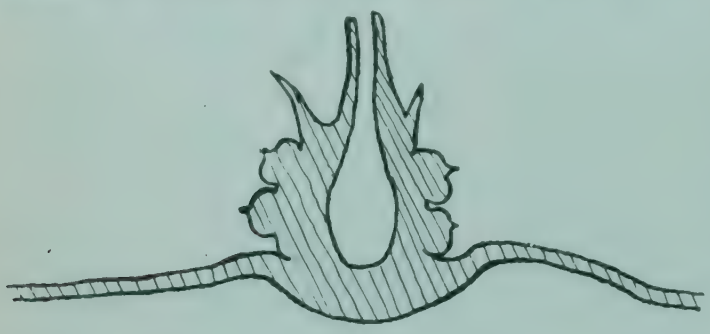


FIG. 124. CROSS SECTION THROUGH A PINEAPPLE GALL

HYMENOPTERA

Tenthredinidae

cerasi Linn., *Caliroa* (Pear and cherry slug)

The sluglike larvae of *Caliroa cerasi* were in a few localities so abundant that they defoliated a few native hawthorns and injured a number of others. In August, 1918, several trees on the Cornell University campus were completely defoliated, while neighboring trees were untouched by the larvae.

Sawfly No. 1

On June 23, 1918, a leaf of *Crataegus pruinosa* was found with a row of fourteen eggs inserted in the margin. The eggs hatched on June 28, and a row of little green larvae, with large, black heads and many black dots scattered over the body, began to feed gregariously on the edge of the leaf. All of them died within a few days.

Sawfly No 2

On May 24, 1918, several medium-sized sawfly larvae, bright green all over, were seen eating separately on the edges of *Crataegus punctata* leaves.

Sawfly No. 3

Sawfly larvae, with red heads and yellow bodies marked with black lines and dots, were found feeding on the leaves of *Crataegus punctata* in late August, 1918. They were feeding two or three together on a leaf, and fifteen larvae were taken from one tree. When they became about 2 centimeters long, on September 1 and 2, they spun brown cocoons on the ground among débris. A tree with ten larvae of the same species

feeding on it was found on September 19, 1919, and these larvae spun cocoons on the ground on September 22 and 23.

Sawfly No. 4

A few larvae $2\frac{1}{2}$ centimeters long, with black heads and yellow bodies marked with black lines and dots, were found feeding on the foliage of *C. pruinosa* in July and August, 1918. They spun brown cocoons on top of the ground, in the cages.

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PIERCE, W. DWIGHT. The insect enemies of the cotton boll weevil. U. S. Ent. Bur. Bul. 100:1–99. 1912.

THEOBALD, FRED V. The app'e blossom weevil. *In* The insect and other allied pests of orchard, bush, and hothouse fruits, and their prevention and treatment, p. 104–110. 1909.

WELLHOUSE, WALTER H. *Xanthonia villosula* Melsh. injuring forest trees. Journ. econ. ent. **12**:396–397. 1919.

Memoir 52, *Studies in Pollen, with Special Reference to Longevity*, the fourth preceding number in this series of publications, was mailed on March 9, 1922.

CATALOG OF INSECTS INJURIOUS TO CRATAEGUS[2]

ACARINA

armatus Can., *Epetrimerus*.....Fam. *Phyllocoptidae*
Host — *Crataegus oxyacantha.*
Injury — Forms galls on leaves.
Distribution — Europe.
References — Houard, C. Les zoocecides des plantes d'Europe, 1:515. 1908.
Theobald, F. V. Board Agr. London. Journ. 20:106–116. 1913.

calycobius Nal., *Eriophyes*.....Fam. *Eriophyidae*
Host — *Crataegus oxyacantha.*
Injury — Deforms leaf buds and causes them to remain closed.
Distribution — Europe.
Reference — Ross, H. Die Pflanzengallen Mittel- und Nordeuropas, p. 132. 1911.

crataegi Can., *Eriophyes*.....Fam. *Eriophyidae*
Host — *Crataegus oxyacantha.*
Injury — Forms galls on leaves, on both upper and lower surfaces. A single leaf may have a hundred galls on it.
Distribution — Europe.
Reference — Connold, E. T. British vegetable galls, p. 132. 1902.

crataegi-vermiculus Walsh, *Eriophyes*.....Fam. *Eriophyidae*
Hosts — *Crataegus tomentosa, C. crus-galli.*
Injury — Forms curled leaf galls on upper side of leaf.
Distribution — North America.
Reference — Walsh, B. D. Ent. Soc. Philadelphia. Proc. 6:227. 1866.

goniothorax Nal., *Eriophyes*.....Fam. *Eriophyidae*
Synonyms — *Erineum oxyacanthae* Am., *Erineum clandestinum* Grev.
Host — *Crataegus oxyacantha.*
Injury — Forms galls on edges of lobes of leaf, causing them to curl downward and become thickened.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 213. 1872.
Connold, E. T. British vegetable galls, p. 138. 1902.

pilosus Can., *Tetranychus*.....Fam. *Tetranychidae*
Hosts — Crataegus, Malus, Pyrus, Prunus.
Injury — Feeds on leaves, causing them to turn brownish.
Distribution — Europe, North America.
Reference — Caesar, L. Can. ent. 47:57. 1915.

pyracanthae Link., *Eriophyes*.....Fam. *Eriophyidae*
Hosts — *Crataegus punctata, C. pyracantha.*
Injury — Makes galls on leaves. Galls almost flat, reddish, covered with many fine, capitate hairs.
Distribution — North America.
Reference — Chadwick, G. H. New York State Mus. Bul. 124:131. 1908.

pyri Pagst., *Eriophyes* (Pear leaf blister mite).....Fam. *Eriophyidae*
Hosts — Pyrus, Malus, Crataegus, Cydonia, Sorbus, Amelanchier.
Injury — Makes yellowish or reddish blisters on leaves.

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[2] The insects are grouped according to order, and arranged alphabetically by species within the order

Distribution — Europe, North America, Australia.
References — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 227. 1914.
Wilson, H. F. Oregon Agr. Exp. Sta. Bien. crop pest and hort. rept. 2:123. 1915.

telarius Linn., *Tetranychus* (Red spider) ..... Fam. *Tetranychidae*
(See page 1051.)

Eriophyes sp. (Hawthorn serpentine gall of Jarvis) ..... Fam. *Eriophyidae*
Host — Crataegus.
Injury — Makes long, irregular, wavy galls on upper surface of leaves.
Distribution — North America.
Reference — Jarvis, T. D. Ent. Soc. Ont. Rept. 37:60. 1906.
(Figs. 102 and 103, pages 1052 and 1053.)

ORTHOPTERA

atlanis Riley, *Melanoplus* ..... Fam. *Acridiidae*
(See page 1054.)

bivittatus Say, *Melanoplus* ..... Fam. *Acridiidae*
(See page 1054.)

femur-rubrum De Geer, *Melanoplus* ..... Fam. *Acridiidae*
(See page 1054.)

niveus De Geer, *Oecanthus* (Snowy tree cricket) ..... Fam. *Gryllidae*
Hosts — Malus, Rubus, Salix, Crataegus, Ulmus, Quercus, and other species.
Injury — Female slits bark to deposit eggs. Slits give entrance to cankers and cause scars on branches.
Distribution — North America, Cuba.
Reference — Parrott, P. J., and Fulton, B. B. New York (Geneva) Agr. Exp. Sta. Bul. 388. 1914.

ODONATA

viridis v. d. Lind., *Lestes* ..... Fam. *Agrionidae*
Hosts — *Crataegus oxyacantha* and other species.
Injury — Oviposition punctures in twigs cause galls to form.
Distribution — Europe.
References — Pierre, P. F. M. Rev. sci. Bourbonnais 15:181. 1902.
Houard, C. Les zoocecides des plantes d'Europe, 1:514. 1908.

HEMIPTERA

aceris Sign., *Phenacoccus* ..... Fam. *Coccidae*
Hosts — *Crataegus oxyacantha* and many other woody plants.
Injury — Sucks sap from tender bark of young shoots and calloused wounds. Sometimes seriously injures grape.
Distribution — Europe.
References — Lindinger, L. Die Schildläuse, p. 214. 1912.
Carpenter, G. H. Roy. Dublin Soc. Econ. proc. 2:142–160. 1914.

ambiguus Fall., *Psallus* ..... Fam. *Miridae*
Hosts — Crataegus, Pyrus, Malus, Alnetis.
Distribution — Europe.
References — Reuter, O. M. Hemiptera gymnocerata Europae 1:105. 1878.
Leonardi, G. Gli insetti 4:98. 1901.

bakeri Cowen, *Aphis* (Clover aphid) ..... Fam. *Aphididae*
Hosts — Malus, Crataegus, clover.
Injury — Sucks juice from opening buds of fruit trees.
Distribution — North America.
References — Quaintance, A. L., and Baker, A. C. U. S. Agr. Dept. Farmers' bul. 804:15. 1917.
Patch, E. M. Maine Agr. Exp. Sta. Bul. 270:49. 1918.

bellula Gibson, *Corythucha* ..... Fam. *Tingitidae*
Hosts — *Crataegus neofluvialis, C. punctata, C. albicans, Alnus incana, Ribes oxyacanthoides.*
Injury — Both young and adult bugs suck juice from leaves, causing them to turn brown and drop off.
Distribution — Northeastern United States, Canada.
References — Gibson, E. H. Amer. Ent. Soc. Trans. 44:93. 1918.
Wellhouse, W. H. Journ. econ. ent. 12:441. 1919.
(Plates LXXII and LXXIII, pages 1057 and 1059.)

betulae Bär., *Epidiaspis* (European pear scale) ..... Fam. *Coccidae*
Synonyms — *Epidiaspis leperi* Sign., *E. piricola* De Geer, *Diaspis piri* Colv.
Hosts — Pyrus, Malus, Prunus, Crataegus, and other species.
Injury — Very injurious to young twigs and branches of apple and pear in southern Europe, where the bark becomes incrusted.
Distribution — South and middle Europe, United States.
References — Lindinger, L. Die Schildläuse, p. 213. 1912.
Essig, E. O. Injurious and beneficial insects of California, p. 172. 1915.

bituberculatum Targ., *Lecanium* ..... Fam. *Coccidae*
Hosts — *Crataegus oxyacantha*, Malus, Pyrus.
Injury — Sucks sap from bark, sometimes killing young trees.
Distribution — Europe, North America.
References — Sorauer, P. Handbuch der Pflanzenkrankheiten 3:695. 1913.
Dietz, H. F., and Morrison, H. Indiana State Ent. Ann. rept. 8:254. 1916.

brevis Sand., *Aphis* (Long-beaked clover aphid) ..... Fam. *Aphididae*
Hosts — Crataegus, Cydonia, Pyrus, clovers, sweet pea.
Injury — Curls and turns purplish the terminal leaves of Crataegus shoots during June.
Distribution — United States.
Reference — Patch, E. M. Journ. agr. res. 3:431. 1915.

brunnea Gibson, *Corythucha* ..... Fam. *Tingitidae*
Host — Crataegus.
Injury — Sucks juice from foliage.
Distribution — Southern United States.
Reference — Gibson, E. H. Amer. Ent. Soc. Trans. 44:93. 1918.

bubalis Fabr., *Ceresa* (Buffalo tree hopper) ..... Fam. *Membracidae*
Hosts — Malus, Crataegus, and other species.
Injury — Adult makes incisions in branches for oviposition. Incisions are slow to heal and allow entrance of borers and fungi.
Distribution — North America.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 535. 1890.
Hodgkiss, H. E. New York (Geneva) Agr. Exp. Sta. Tech. bul. 17:92. 1910.

clitellarius Say, *Thamnotettix* ..... Fam. *Cicadellidae*
(See page 1061.)

coccinea Först., *Graphocephala*.....Fam. *Cicadellidae*
(See page 1061.)

communis Knight, *Lygus*.....Fam. *Miridae*
(See page 1054.)

corni Bouché, *Lecanium* (European fruit lecanium).....Fam. *Coccidae*
Hosts — Crataegus, Malus, Prunus, and other species.
Injury — May suck so much sap from branches as to kill them, but commoner injury is due to growth of sooty fungus over sticky secretion which the insects drop on foliage, fruit, and branches.
Distribution — Europe, North America.
References — Sorauer, P. Handbuch der Pflanzenkrankheiten 3:695. 1913.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 261. 1914.

corrugatans Sir., *Pemphigus* (Woolly thorn aphis).....Fam. *Aphididae*
Hosts — Crataegus, Amelanchier, Pyrus, Cydonia.
Injury — Distorts leaves into a rolled curl.
Distribution — North America.
References — Patch, E. M. Maine Agr. Exp. Sta. Bul. 233. 1914.
Quaintance, A. L., and Baker, A. C. U. S. Agr. Dept. Farmers' bul. 804:19. 1917.

coryli Linn., *Lecanium*.....Fam. *Coccidae*
Synonyms — *Eulecanium pyri* Schr., *Lecanium capreae* Linn.
Hosts — Malus, Crataegus, Pyrus, and other species.
Injury — Sucks sap from bark, not commonly injurious.
Distribution — Europe, North America.
References — Theobald, F. V. Insect pests of fruits, p. 175. 1909.
Lindinger, L. Die Schildläuse, p. 216. 1912.

costalis Flor., *Psylla*.....Fam. *Psyllidae*
Hosts — Malus, Crataegus, Sorbus, Quercus.
Distribution — Europe.
Refere ce — Harrison, J. W. H. Naturalist (London), no. 707, p. 400. 1915.

crataegarium Walk., *Macrosiphum*.....Fam. *Aphididae*
Host — *Crataegus oxyacantha*.
Distribution — Enlgand.
References — Walker, F. Ann. mag. nat. hist. **6**:46. 1850.
Theobald, F. V. Journ. econ. biol. 8:142. 1913.

crataegi Kalt., *Aphis*.....Fam. *Aphididae*
Synonyms — *Aphis pyri* Boyer, *A. crataegi* Koch, *A. ranunculi* Kalt.
Hosts — *Crataegus oxyacantha, C. azarolus*, Malus, Ranunculus.
Injury — Curls, discolors, and blisters leaves on terminal shoots.
Distribution — Europe.
References — Dobrovliansky, V. V. Biology of aphids of tree and bush fruits (Kiev). 1913.
Van der Goot, P. Holländischen Blattläuse, p. 174. 1915.
Theobald, F. V. Entomologist 48:259. 1915.

crataegi Fitch, *Glossonotus* (Hawthorn tree hopper).....Fam. *Membracidae*
Hosts — Crataegus, Malus, Cydonia.
Distribution — North America.
References — Fitch, A. Third annual report on noxious insects of New York, p. 334. 1856.
Funkhouser, W. D. Cornell Univ. Agr. Exp. Sta. Memoir 11:248. 1917.

crataegi VanD., *Idiocerus*.....Fam. *Cicadellidae*
Host — Crataegus.
Injury — Adults and young suck juice from foliage.
Distribution — North America.
Reference — Van Duzee, E. P. Can. ent. **22**:110. 1890.

crataegi Monell, *Macrosiphum*.....Fam. *Aphididae*
Hosts — *Crataegus punctata*, *C. coccinea*, *C. oxyacantha*.
Injury — Sucks juice from lower side of leaves and from tender twigs. Leaves curl downward and in severe infestations trees may be defoliated.
Distribution — North America.
Reference — Patch, E. M. Maine Agr. Exp. Sta. Bul. 233:255. 1914.
(Fig. 108, page 1063.)

crataegi Tullgr., *Prociphilus*.....Fam. *Aphididae*
Hosts — *Crataegus oxyacantha*, Malus.
Injury — Curls and discolors leaves and sometimes injures blossoms.
Distribution — Europe.
Reference — Van der Goot, P. Holländischen Blattläuse, p. 450. 1915.

crataegi Schr., *Psylla*.....Fam. *Psyllidae*
Synonym — *Chermes quercus* Thoms.
Hosts — *Crataegus oxyacantha*, *Quercus* sp.
Injury — Causes small red blisters to form on upper side of leaves.
Distribution — Europe.
Reference — Aulmann, G. Psyllidarum catalogus, p. 13. 1913.

crataegi Dgl., *Typhlocyba*.....Fam. *Cicadellidae*
Hosts — *Crataegus oxyacantha*, apple (?).
Injury — Nymphs and adults suck juice from foliage, but commonly they are not numerous enough to cause much injury.
Distribution — Europe.
References — Douglas, J. W. Ent. mo. mag. **12**:203. 1876.
Melichar, L. Cicadinen von Mittel-Europe, p. 348. 1896.

crataegiella Theobald, *Aphis*.....Fam. *Aphididae*
Synonym — *Aphis crataegi* Buck.
Host — *Crataegus oxyacantha*.
Injury — Curls and discolors leaves of terminal shoots, which turn reddish brown.
Distribution — Europe.
References — Buckton, G. B. Monograph of British aphides, **2**:35. 1879.
Theobald, F. V. List of Aphididae of Hastings District, p. 9. 1912.

crataegifoliae Fitch, *Aphis*.....Fam. *Aphididae*
Hosts — *Crataegus punctata*, *C. coccinea*, *C. oxyacantha*, *C. tomentosa*, Cydonia, legumes.
Injury — Curls and discolors leaves and young shoots, turning them purplish.
Distribution — North America.
Reference — Quaintance, A. L., and Baker, A. C. U. S. Agr. Dept. Farmers' bul. 804:18. 1917.

crataegus-coccinea Rafin., *Aphis*.....Fam. *Aphididae*
Host — *Crataegus coccinea*.
Distribution — North America.
References — Rafinesque, C. S. Amer. mo. mag. and crit. rev. **3**:16. 1818.
Patch, E. M. Maine Agr. Exp. Sta. Bul. 270:48. 1918.

curtisii Fb., *Euscelis*.....Fam. *Cicadellidae*
(See page 1161.)

cydoniae Fitch, *Corythucha*.....Fam. *Tingitidae*
Synonyms — *Corythucha arcuata* Comst., *C. crataegi* O. & D.
Hosts — Crataegus, Cydonia.
Injury — Nymphs and adults suck juice from leaves, causing them to turn brown.
Distribution — North America.
References — Fitch, A. Country gent. **17**:25. 1861.
Comstock, J. H. U. S. Ent. Rept. **1879**:221. 1879.
Gibson, E. H. Amer. Ent. Soc. Trans. **44**:87. 1918.

dearnessi King, *Phenacoccus*.....Fam. *Coccidae*
Synonym — *Phenacoccus betheli* Ckll.
Hosts — Crataegus, Amelanchier.
Distribution — Canada, United States.
Reference — Ferris, G. F. Contribution to knowledge of Coccidae of southwestern United States, p. 68. 1919.

dislocatus Say, *Horcias*.....Fam. *Miridae*
(See page 1054.)

dumetorum Schiff., *Physatocheila*.....Fam. *Tingitidae*
Hosts — *Crataegus oxyacantha, Pyrus communis, Prunus padus, P. spinosa.*
Distribution — Europe, Egypt.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 213. 1872.
Saunders, E. Hemiptera of British Islands, p. 135. 1892.

edentula Buck., *Aphis*.....Fam. *Aphididae*
Host — *Crataegus oxyacantha.*
Distribution — Europe.
Reference — Buckton, G. B. Monograph of British aphides, **2**:39. 1879.

fitchi VanD., *Idiocerus* (Black apple leaf hopper).....Fam. *Cicadellidae*
Synonym — *Idiocerus maculipennis* Fitch.
Hosts — Crataegus, Malus, Pyrus.
Injury — Adults and young suck juice from foliage. Not commonly injurious.
Distribution — North America.
References — Van Duzee, E. P. Catalog of Hemiptera, p. 580. 1916.
Brittain, W. H., and Saunders, L. G. Can. ent. **49**:149. 1917.

flavicephala Goding, *Ophiderma*.....Fam. *Membracidae*
(See page 1063.)

furfura Fitch, *Chionaspis* (Scurfy scale).....Fam. *Coccidae*
Hosts — About 25 tree species, including Crataegus, Malus, Pyrus, Cydonia, Sorbus.
Injury — Occasionally incrusts bark of trees and greatly weakens or kills them.
Distribution — North America.
References — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 176. 1914.
Essig, E. O. Injurious and beneficial insects of California, p. 158. 1915.

hederae Vall., *Aspidiotus*.....Fam. *Coccidae*
Synonym — *Aspidiotus nerii* Bouché.
Hosts — Many woody and herbaceous plants, including *Crataegus azarolus.*
Distribution — Europe, Asia, North Africa (on Crataegus in Algeria), North America.
References — Lindinger, L. Die Schildläuse, p. 213. 1912.
Sorauer, P. Handbuch der Pflanzenkrankheiten **3**:689. 1913.

lachrymalis Fb., *Idiocerus*.....Fam. *Cicadellidae*
(See page 1061.)

lanigera Hausm., *Eriosoma* (Woolly aphis) ..... Fam. *Aphididae*
Synonyms — *Eriosoma crataegi* Oest., *Schizoneura americana* Riley.
Hosts — Crataegus, Malus, *Ulmus americana.*
Injury — Sucks sap from tender shoots, branches, and roots, often stunting growth.
Distribution — North America, Europe, Africa, Australia, South America.
References — Theobald, F. V. Insect pests of fruits, p. 141. 1909.
Baker, A. C. U. S. Agr. Dept. Rept. 101. 1915.
Becker, G. G. Journ. econ. ent. 11:245. 1918.
(Fig. 109, page 1064.)

lineatus Linn., *Philaenus* ..... Fam. *Cicadellidae*
(See page 1061.)

mali LeB., *Empoasca* (Apple leaf hopper) ..... Fam. *Cicadellidae*
(See page 1061.)

mali Schmid., *Psylla* ..... Fam. *Psyllidae*
Synonym — *Psylla crataegicola* Först.
Hosts — *Crataegus oxyacantha,* Malus, Pyrus, Sorbus, Quercus, Ulmus, Corylus.
Injury — Nymphs suck juice from foliage and blossoms, and prevent setting of fruit.
Distribution — Europe, Asia, Nova Scotia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 213. 1872.
Theobald, F. V. Insect pests of fruits, p. 153. 1909.
Brittain, W. H. Journ. econ. ent. 15:96. 1922.

malinus Reuter, *Heterocordylus* (Dark apple redbug) ..... Fam. *Miridae*
Hosts — Crataegus, Malus.
Injury — Nymphs and adults puncture leaves and fruit to suck juice. Cause dimples in fruit, which deform it.
Distribution — Northeastern United States, Canada.
References — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 28. 1914.
Cushman, R. A. Ent. Soc. Washington. Proc. 18:196. 1916.

marutae Oest., *Aphis* ..... Fam. *Aphididae*
Hosts — Crataegus, *Anthemis cotula.*
Distribution — North America.
References — Oestlund, O. W. Aphididae of Minnesota, p. 40. 1886.
Hunter, 1901, p. 101. (*Cited by* Patch, E. M. Maine Agr. Exp. Sta. Bul. 270:49. 1918.)

melanoneura Först., *Psylla* ..... Fam. *Psyllidae*
Synonym — *Psylla crataegi* Först.
Hosts — *Crataegus oxyacantha,* Quercus, and other species.
Distribution — Europe, Asia.
References — Aulmann, G. Psyllidarum catalogus, p. 20. 1913.
Harrison, J. W. H. Naturalist (London), no. 707, p. 400. 1915.

mendax Reuter, *Lygidea* (Bright apple redbug) ..... Fam. *Miridae*
Hosts — Malus, Crataegus.
Injury — Nymphs and adults puncture leaves and fruit to suck juice, and cause dimples in fruit.
Distribution — Northeastern United States, Canada.
References — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 28. 1914.
Cushman, R. A. Ent. Soc. Washington. Proc. 18:196. 1916.

mespili v.d.G., *Ovatus* ..... Fam. *Aphididae*
Hosts — *Crataegus oxyacantha, Mespilus germanica.*

Injury — Sucks sap from tender shoots and leaves.
Distribution — Europe.
Reference — Van der Goot, P. Holländischen Blattläuse, p. 136. 1915.

nigrofasciatum Perg., *Lecanium* (Terrapin scale) ..... Fam. *Coccidae*
Hosts — Prunus, Acer, Malus, Crataegus, Tilia, Platanus, and other species.
Injury — Sucks sap from bark and secretes much sticky liquid, which covers surface of branches, foliage, and fruit and on which a sooty fungus grows, thus rendering fruit unsalable.
Distribution — North America.
References — Felt, E.P. New York State Mus. Memoir 8[1]:201. 1905.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 293. 1914.

obliqua Say, *Erythroneura* ..... Fam. *Cicadellidae*
(See page 1061.)

oleae Colvee, *Parlatoria* ..... Fam. *Coccidae*
Hosts — Many woody plants, including *Crataegus germanica.*
Injury — May incrust the bark, and sometimes the leaves and the fruit, of trees of the genera Citrus, Pyrus, and Olea especially.
Distribution — Mediterranean region.
References — Lindinger, L. Die Schildläuse, p. 213. 1912.
Sorauer, P. Handbuch der Pflanzenkrankheiten 3:694. 1913.

olivaceus Fabr., *Deraeocoris* ..... Fam. *Miridae*
Synonym — *Capsus medius* Kirschb.
Hosts — Malus, Crataegus, Prunus, Corylus.
Injury — Sucks juice from foliage.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 213. 1872.
Reuter, O. M. Hemiptera gymnocerata Europae 5:30. 1896.

ornatus VanD., *Orthotylus* ..... Fam. *Miridae*
(See page 1055.)

ostreiformis Curt., *Aspidiotus* (European fruit-tree scale) ..... Fam. *Coccidae*
Synonym — *Aspidiotus oxyacanthae* Sign.
Hosts — Malus, Prunus, Pyrus, Crataegus, and many other woody plants.
Injury — May completely incrust the bark and kill the tree.
Distribution — Europe, Asia Minor, North America.
References — Theobald, F. V. Insect pests of fruits, p. 386. 1909.
Lindinger, L. Die Schildläuse, p. 213. 1912.

ostryae Knight, *Lygus* ..... Fam. *Miridae*
(See page 1055.)

oxyacanthae Schr., *Myzus* ..... Fam. *Aphididae*
Synonym — *Aphis oxyacanthae* Koch.
Hosts — *Crataegus oxyacantha,* Pyrus, Malus, Prunus.
Injury — Sucks juice from leaves, causing yellow or red swellings on them and making them curl.
Distribution — Europe.
References — Koch, C. L. Pflanzenläuse, p. 55. 1857.
Ross, H. Die Pflanzengallen Mittel- und Nordeuropas, p. 132. 1911.

padi Linn., *Rhopalosiphum* ..... Fam. *Aphididae*
Synonyms — *Aphis avenae* Fabr., *Aphis padi* Kalt.
Hosts — *Prunus padus,* Crataegus, Malus, Pyrus, grasses.

Injury — Sucks juice from opening buds of fruit trees in early spring.
Distribution — Europe, North America.
References — Leonardi, G. Gli insetti 4:228. 1901.
Baker, A. C. Journ. agr. res. 18:311. 1919.

pallidus Fb., *Idiocerus* ..... Fam. *Cicadellidae*
(See page 1062.)

pellucida Uhl., *Diaphnidia* ..... Fam. *Miridae*
(See page 1055.)

peregrina Först., *Psylla* ..... Fam. *Psyllidae*
Synonym — *Psylla crataegicola* Flor.
Hosts — *Crataegus oxyacantha, Carpinus betulus.*
Injury — Sucks juice from young shoots and foliage.
Distribution — Europe, Asia.
Reference — Aulmann, G. Psyllidarum catalogus, p. 22. 1913.

perniciosus Comst., *Aspidiotus* (San José scale) ..... Fam. *Coccidae*
Hosts — Many woody plants, including Crataegus and other Malaceae.
Injury — May incrust bark and kill trees in favorable weather.
Distribution — Asia, North America, South America, Australia, Hawaii.
References — Sorauer, P. Handbuch der Pflanzenkrankheiten 3:690. 1913.
Glenn, P. A. State Ent. Illinois. Rept. 28:87. 1915.

piri Licht., *Aspidiotus* ..... Fam. *Coccidae*
Hosts — Pyrus, Malus, Crataegus, Fraxinus, Prunus.
Injury— May incrust branches and thus weaken or kill them.
Distribution — Europe, Asia Minor.
References — Lindinger, L. Die Schildläuse, p. 214. 1912.
Sorauer, P. Handbuch der Pflanzenkrankheiten 3:690. 1913.

pomi De Geer, *Aphis* (Green apple aphis) ..... Fam. *Aphididae*
Synonyms — *Aphis mali* Fabr., *A. oxyacanthae* Schr.
Hosts — Malus, Crataegus, grasses.
Injury — Sucks sap, causing leaves to curl, but no discoloration appears.
Distribution — Europe, North America.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 202. 1872.
Matheson, R. Cornell Univ. Agr. Exp. Sta. Memoir 24:686. 1919.

pratensis Linn., *Lygus* ..... Fam. *Miridae*
(See page 1055.)

provancheri VanD., *Idiocerus* ..... Fam. *Cicadellidae*
Hosts — Crataegus, Malus, Pyrus, Cydonia.
Injury — Nymphs and adults suck juice from foliage.
Distribution — North America.
References — Leonard, M. D. Journ. econ. ent. 8:415. 1915.
Van Duzee, E. P. Catalog of Hemiptera, p. 580. 1916.

pruinosum Coq., *Lecanium* (Frosted scale) ..... Fam. *Coccidae*
Hosts — Many woody plants, including Crataegus.
Injury — Principal injury from smutty fungus growing on honeydew secreted by insects on fruit and foliage.
Distribution — North America.
References — Sanders, J. G. Journ. econ. ent. 2:442. 1909.
Essig, E. O. Injurious and beneficial insects of California, p. 149. 1915.

prunifoliae Fitch, *Rhopalosiphum* (Apple bud aphis) ..... Fam. *Aphididae*
Synonyms — *Aphis avenae* (of American authors), *Aphis fitchii* Sand.

Hosts — Malus, Pyrus, Crataegus, Prunus, many grasses.
Injury — Sucks juice from opening buds of trees in spring.
Distribution — North America.
References — Quaintance, A. L. U. S. Ent. Bur. Circ. 81. 1907.
Baker, A. C. Journ. agr. res. 18:311. 1919.

pumilus Uhl., *Ceratocapsus* ..... Fam. *Miridae*
Synonym — *Melinna pumila* Uhl.
Hosts — Crataegus, Salix.
Injury — Adult sucks sap from foliage.
Distribution — Eastern United States.
Reference — Uhler, P. R. Ent. Amer. 3:69. 1887.

pyri Fitch, *Prociphilus* (Pear root aphis) ..... Fam. *Aphididae*
Hosts — Pyrus, Crataegus, Malus.
Injury — Sucks sap from roots.
Distribution — Eastern North America.
References — Quaintance, A. L., and Baker, A. C. U. S. Agr. Dept. Farmers' bul. 804:19. 1917.
Wilson, H. F., and Vickery, R. A. Wisconsin Acad. Sci., Arts, and Letters. Trans. 19:140. 1918.

querci Fitch, *Empoa* ..... Fam. *Cicadellidae*
(See page 1062.)

rosae Linn., *Empoa* (Rose leaf hopper) ..... Fam. *Cicadellidae*
Hosts — Rosa, Malus, Pyrus, Prunus, Crataegus, Cydonia, and other species.
Injury — Nymphs and adults suck juice from lower leaves of trees, causing yellowing of foliage and in some cases defoliation.
Distribution — Europe, North America.
Reference — Ackerman, A. J. U. S. Agr. Dept. Bul. 805:20. 1919.

rumicis Linn., *Aphis* ..... Fam. *Aphididae*
Hosts — Many herbs and woody plants, including *Crataegus oxyacantha* and pear.
Injury — Sucks juice from foliage in spring and fall.
Distribution — Europe, North America.
References — Börner. Nat. Ver. Bremen. Abhandl. 23:152. 1914.
Van der Goot, P. Holländischen Blattläuse, p. 220. 1915.

rusci Linn., *Ceroplastes* ..... Fam. *Coccidae*
Hosts — Many plants, including Crataegus.
Injury — Sucks juice from bark, leaves, and fruit.
Distribution — Mediterranean region.
References — Lindinger, L. Die Schildläuse, p. 214. 1912.
Sorauer, P. Handbuch der Pflanzenkrankheiten 3:695. 1913.

saliceti Först., *Psylla* ..... Fam. *Psyllidae*
Hosts — Salix, *Crataegus oxyacantha.*
Injury — Sucks juice from foliage.
Distribution — Europe, Asia, Japan.
Reference — Aulmann, G. Psyllidarum catalogus, p. 26. 1913.

seminudus Say, *Eutettix* ..... Fam. *Cicadellidae*
(See page 1062.)

sorbi Kalt., *Aphis* (Rosy apple aphis) ..... Fam. *Aphididae*
Synonym — *Aphis malifoliae* Fitch.
Hosts — Malus, Pyrus, Crataegus, Sorbus, Plantago.
Injury — Curls leaves and deforms fruit.

Distribution — Europe, North America.
References — Van der Goot, P. Holländischen Blattläuse, p. 177. 1915.
Matheson, R. Cornell Univ. Agr. Exp. Sta. Memoir 24:718. 1919.

suturalis Fb., *Idiocerus*.....Fam. *Cicadellidae*
(See page 1062.)

taurina Fitch, *Ceresa*.....Fam. *Membracidae*
(See page 1063.)

ulmi Linn., *Lepidosaphes* (Oyster-shell scale).....Fam. *Coccidae*
Synonym — *Mytilaspis pomorum* Bouché.
Hosts — Many woody plants, including Crataegus.
Injury — Sucks juice from bark and foliage.
Distribution — Europe, Asia, Africa, Australia, North America, South America, Hawaii.
References — Theobald, F. V. Insect pests of fruits, p. 170. 1909.
Sorauer, P. Handbuch der Pflanzenkrankheiten 3:692. 1913.

ulmi Geof., *Tetraneura*.....Fam. *Aphididae*
Hosts — Ulmus, *Crataegus oxyacantha*, many grasses.
Injury — Sucks juice from leaves, causing galls to form on upper surface.
Distribution — Europe.
References — Van der Goot, P. Holländischen Blattläuse, p. 484. 1915.
Patch, E. M. Maine Agr. Exp. Sta. Bul. 270:49. 1918.

univittatus Knight, *Lygus*.....Fam. *Miridae*
Host — Crataegus.
Injury — Adults suck juice and puncture fruit and tender foliage.
Distribution — Northeastern United States.
Reference — Knight, H. H. Brooklyn Ent. Soc. Bul. 14:21. 1919.

urticae Linn., *Trioza*.....Fam. *Psyllidae*
Hosts — Urtica, *Crataegus oxyacantha*.
Injury — Sucks juice from foliage.
Distribution — Europe, Asia.
References — Aulmann, G. Psyllidarum catalogus, p. 56. 1913.
Harrison, J. W. H. Naturalist (London), no. 707, p. 400. 1915.

vanduzei Gill., *Eupteryx*.....Fam. *Cicadellidae*
(See page 1062.)

vitis Linn., *Pulvinaria* (Cottony scale).....Fam. *Coccidae*
Synonyms — *Pulvinaria betulae* Linn., *P. innumerabilis* Rath., *P. oxyacanthae* Linn.
Hosts — Many woody plants, including Crataegus.
Injury — Sucks sap from bark and tender shoots.
Distribution — Europe, America, Africa, Asia Minor.
Reference — Lindinger, L. Die Schildläuse, p. 215. 1912.

vulgaris Fb., *Lamenia*.....Fam. *Cicadellidae*
(See page 1063.)

THYSANOPTERA

tritici Fitch, *Euthrips*.....Fam. *Thrypidae*
(See page 1066.)

COLEOPTERA

aeneovirens Marsh, *Rhynchites*, var. *punctatus* Oliv.....Fam. *Curculionidae*
Host — *Crataegus oxyacantha*.
Distribution — Europe.
Reference — Bargagli, P. Rincofori Europei, p. 181. 1883.

aenescens Lec., *Magdalis* (Bronze apple weevil) ..... Fam. *Curculionidae*
Hosts — Malus, Crataegus, Prunus.
Injury — Larva tunnels under bark, sometimes killing tree. Adults feed on leaves.
Distribution — Northwestern United States, Canada.
References — Chittenden, F. H. U. S. Ent. Bur. Bul. 22:37. 1900.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 199. 1914.

aequatus Linn., *Rhynchites* ..... Fam. *Curculionidae*
Hosts — Crataegus, Malus, Prunus, Sorbus.
Injury — Beetles puncture fruit buds and leaves in feeding.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 181. 1872.
Bargagli, P. Rincofori Europei, p. 181. 1883.

aerosus Melsh., *Brachys* ..... Fam. *Buprestidae*
(See page 1066.)

albida Lec., *Syneta* ..... Fam. *Chrysomelidae*
Hosts — Malus, Pyrus, Cydonia, Crataegus, Prunus, Corylus, and other species.
Injury — Beetles feed on flowers and foliage, sometimes defoliating young trees.
Distribution — Western United States.
References — Wilson, H. F., and Moznette, G. F. Oregon Agr. Exp. Sta. Bien. crop pest and hort. rept. 2:96. 1915.

alpina Linn., *Rosalia* ..... Fam. *Cerambycidae*
Hosts — *Crataegus oxyacantha*, *Fagus* sp.
Injury — Larva tunnels under bark, girdling branches, and then enters solid wood.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.
Holeczek, A. Ent. Nachr. 13:308. 1887.

auratus Scop., *Rhynchites* ..... Fam. *Curculionidae*
Synonym — *Rhynchites bacchus* Oliv.
Hosts — *Crataegus oxyacantha*, *Prunus spinosa*, Malus.
Injury — Beetles cut off petioles of leaves, and larvae feed in fruit.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 153. 1872.
Bargagli, P. Rincofori Europei, p. 183. 1883.

bacchus Linn., *Rhynchites* (Purple apple weevil) ..... Fam. *Curculionidae*
Hosts — Malus, Crataegus.
Injury — Larvae feed in fruit, much like codling moth.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.
Theobald, F. V. Insect pests of fruits, p. 121. 1909.

barbicornis Lat., *Magdalis* (Apple stem piercer) ..... Fam. *Curculionidae*
Hosts — Malus, Cydonia, Crataegus.
Injury — Larvae tunnel under bark, causing discolored, sunken areas.
Distribution — Europe, United States (New York and Massachusetts), imported recently.
References — Henschel, G. A. O. Die schädlichen forst- und obstbaum Insekten, p. 94. 1895.
Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 257. 1916.
Pierce, W. D. Manual of dangerous insects, p. 132. 1917.

bipunctatus Linn., *Cryptocephalus* ..... Fam. *Chrysomelidae*
Hosts — Crataegus, Corylus, Salix, Betula.

Injury — Beetles eat holes in foliage.
Distribution — Europe.
References — Redtenbacher, L. Fauna Austriaca. Die Käfer, p. 901. 1858.
Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.

borealis Shev., *Dibolia*.....Fam. *Chrysomelidae*
(See page 1067.)

calva Lec., *Limnobaris*.....Fam. *Curculionidae*
Host — Crataegus.
Distribution — Eastern United States.
Reference — Hamilton, J. Amer. Ent. Soc. Trans. **22**:377. 1895.

candida Fabr., *Saperda* (Round-headed apple-tree borer).....Fam. *Cerambycidae*
Synonym — *Saperda bivittata* Say.
Hosts — Cydonia, Malus, Sorbus, Amelanchier, Pyrus, Crataegus.
Injury — Larvae tunnel under bark of trunk and into sapwood. Not commonly injurious to Crataegus.
Distribution — North America.
References — Glover, T. Manuscript notes from my journal, p. 87. 1877.
Felt, E. P., and Joutel, L. H. New York State Mus. Bul. 74:28. 1904.
Becker, G. G. Arkansas Agr. Exp. Sta. Bul. 146:5. 1918.

carinata Germ., *Haltica*.....Fam. *Chrysomelidae*
(See page 1067.)

caudatus Rossi, *Otiorrhynchus*.....Fam. *Curculionidae*
Host — *Crataegus oxyacantha.*
Distribution — Europe.
References — Marseul, M. S. A. Monographie des Otiorhynchides, p. 127. 1872.
Bargagli, P. Rincofori Europei, p. 63. 1883.

cerasi Linn., *Magdalis*.....Fam. *Curculionidae*
Hosts — *Prunus cerasus, P. padus, Crataegus oxyacantha.*
Injury — Larva burrows under bark.
Distribution — Europe.
References — Redtenbacher, L. Fauna Austriaca. Die Käfer, p. 758. 1858.
Bargagli, P. Rincofori Europei, p. 195. 1883.
Pierce, W. D. Manual of dangerous insects, p. 132. 1917.

coeruleocephalus Schel., *Rhynchites*.....Fam. *Curculionidae*
Hosts — *Crataegus oxyacantha*, Betula, Quercus.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 589. 1872.
Bargagli, P. Rincofori Europei, p. 187. 1883.

colaspidoides Gyll., *Diphucephala*.....Fam. *Scarabaeidae*
Hosts — Prunus, *Crataegus oxyacantha.*
Injury — Beetles appear in swarms, like locusts, and defoliate trees and shrubs.
Distribution — Australia.
References — Insect life **3**:425. 1890.
French, C. Destructive insects of Victoria, **2**:27. 1893.

convergeus Lec., *Xylotrechus*.....Fam. *Cerambycidae*
Host — *Crataegus* sp.
Injury — Larva tunnels in branches.
Distribution — North America.
Reference — LeConte, J. L. Amer. Ent. Soc. Trans. 8:XXIV. 1880.

crataegi Walsh, *Conotrachelus* (Quince curculio) ..... Fam. *Curculionidae*
Hosts — *Crataegus* spp., Cydonia.
Injury — Larvae feed within fruit, partially destroying it.
Distribution — Eastern United States.
References — Riley, C. V. Third Missouri rept., p. 35. 1871.
Slingerland, M. V. Cornell Univ. Agr. Exp. Sta. Bul. 148. 1898.

crataegi Germ., *Otiorrhynchus* ..... Fam. *Curculionidae*
Host — *Crataegus oxyacantha.*
Distribution — Europe.
References — Marseul, M. S. A. Monographie des Otiorhynchides, p. 287. 1872.
Bargagli, P. Rincofori Europei, p. 63. 1883.

crataegi Walsh, *Pseudanthonomus* (Apple weevil) ..... Fam. *Curculionidae*
Hosts — Crataegus, Malus, *Kalmia latifolia.*
Injury — Larvae burrow in fruit, beetles puncture fruit and foliage.
Distribution — Eastern United States, Canada.
References — Brooks, F. E. West Virginia Agr. Exp. Sta. Bul. 126. 1910.
Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 318. 1916.

cretata Newm., *Saperda* (Spotted apple-tree borer) ..... Fam. *Cerambycidae*
Hosts — Malus, Crataegus, Amelanchier.
Injury — Larvae kill branches by girdling and tunneling in sapwood.
Distribution — Eastern North America.
References — Osborn, H. Iowa State Hort. Soc. Trans. **15**:11. 1880.
Hamilton, J. Amer. Ent. Soc. Trans. **22**:369. 1895.
Felt, E. P., and Joutel, L. H. New York State Mus. Bul. 74:50. 1904.

cucumeris Harris, *Epitrix* ..... Fam. *Chrysomelidae*
(See page 1067.)

decipiens Lec., *Anthonomus* ..... Fam. *Curculionidae*
Hosts — Crataegus, cotton (?); beetles in abundance beaten from *Crataegus* sp. by Dr. Hamilton.
Distribution — North America.
Reference — Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 316. 1916.

dorsalis Thunb., *Chalepus* ..... Fam. *Chrysomelidae*
Hosts — Robinia, Malus, Quercus, Crataegus, Rubus, and other species.
Injury — Beetles eat foliage.
Distribution — North America.
Reference — Houser, J. S. Ohio Agr. Exp. Sta. Bul. 332:231. 1918.

dubitans Lec., *Limonius* ..... Fam. *Elateridae*
(See page 1066.)

elongata Fabr., *Dichelonycha* ..... Fam. *Scarabaeidae*
(See page 1066.)

fayi Bland, *Saperda* (Thorn limb borer) ..... Fam. *Cerambycidae*
Hosts — *Crataegus crus-galli, C. tomentosa.*
Injury — Larvae burrow in smaller branches, killing them and producing gall-like swellings which weaken the branches so that they break in winds.
Distribution — Eastern North America.
Reference — Felt, E. P., and Joutel, L. H. New York State Mus. Bul. 74:62. 1904.

femorata Fabr., *Chrysobothris* (Flat-headed apple-tree borer) ..... Fam. *Buprestidae*
Hosts — Many trees, including Crataegus, but especially Quercus, Malus, Prunus.

Injury — Larvae burrow in sapwood of weakened trees.
Distribution — North America.
Reference — Brooks, F. E. U. S. Agr. Dept. Farmers' bul. 1065:5. 1919.

flavicornis Boh. Schn., *Anthonomus* ..... Fam. *Curculionidae*
Hosts — Crataegus, Solanum, dogwood, and other species.
Distribution — North America.
Reference — Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 298. 1916.

flavicornis Clairv., *Ramphus* ..... Fam. *Curculionidae*
Synonym — *Ramphus oxyacanthae* Marsh.
Hosts — Malus, *Crataegus oxyacantha*, Betula, Salix, Prunus, Populus.
Injury — Larvae mine in leaves.
Distribution — Europe.
References — Heyden, C. von. Berlin. ent. Zeit. 6:63. 1862.
Bargagli, P. Rincofori Europei, p. 251. 1883.

foliacea Lec., *Haltica* (Apple flea beetle) ..... Fam. *Chrysomelidae*
Hosts — Malus, Crataegus.
Injury — Beetles and larvae eat many small holes in foliage.
Distribution — North America.
Reference — Murtfeldt, M. E. Insect life 1:74. 1888.

giganteus Krinick., *Rhynchites* ..... Fam. *Curculionidae*
Host — *Crataegus oxyacantha.*
Distribution — Europe, Asia.
References — Desbrochers, L. Monographie des Rhinomaceridae, p. 345. 1869.
Bargagli, P. Rincofori Europei, p. 180, 188. 1883.

helxines Linn., *Crepidodera* ..... Fam. *Chrysomelidae*
Hosts — Crataegus, Salix, Malus, Pyrus, Ulmus, Populus.
Injury — Beetles eat many small holes in leaves.
Distribution — Europe, North America.
References — Blatchley, W. S. Coleoptera of Indiana, p. 1214. 1910.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 205. 1914.

icosandriae Scop., *Rhynchites* ..... Fam. *Curculionidae*
Synonym — *Rhynchites conicus* Ill.
Hosts — *Crataegus oxyacantha*, Malus, Pyrus, Prunus, Sorbus.
Injury — Beetles cut off tender twigs. Serious pest in nurseries.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 154, 207. 1872.
Bargagli, P. Rincofori Europei, p. 188. 1883.

impressifrons Gyll., *Polydrusus* ..... Fam. *Curculionidae*
Hosts — Salix, Populus, Crataegus, Quercus, Malus, Pyrus, Corylus, and other species.
Injury — Beetles eat buds, leaves, and tender twigs in May and June.
Distribution — Europe, New York (imported about 1906).
References — Parrott, P. J., and Glasgow, H. New York (Geneva) Agr. Exp. Sta. Tech. bul. 56:7. 1916.
Pierce, W. D. Journ. econ. ent. 9:424. 1916.

maculicornis Germ., *Phyllobius* (Green leaf weevil) ..... Fam. *Curculionidae*
Hosts — Malus, Pyrus, Prunus, Quercus, Crataegus, Acer.
Injury — Beetle eats into opening buds, and later eats holes in leaves.
Distribution — Europe, Asia.
Reference — Theobald, F. V. Insect pests of fruits, p. 119. 1909.

marginalis Ill., *Systena*.....Fam. *Chrysomelidae*
(See page 1067.)

metasternalis Cr., *Tymnes*.....Fam. *Chrysomelidae*
Host — Crataegus.
Distribution — North America.
Reference — Smith, J. B. Insects of New Jersey, p. 344. 1909.

mixtus Lec., *Anthonomopsis*.....Fam. *Curculionidae*
Hosts — Crataegus, Prunus.
Distribution — North America.
Reference — Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 286. 1916.

multipunctata Say, *Calligrapha*.....Fam. *Chrysomelidae*
Host — Crataegus.
Distribution — North America.
Reference — Blatchley, W. S. Coleoptera of Indiana, p. 1158. 1910.

naso Lec., *Conotrachelus*.....Fam. *Curculionidae*
Hosts — Crataegus, *Quercus virginiana.*
Injury — Larva feeds in fruit.
Distribution — North America.
References — Hamilton, J. Can. ent. **21**:34. 1889.
Pierce, W. D. Nebraska State Bd. Agr. Ann. rept. **1906–07**:275. 1907.

nebulosus Lec., *Anthonomus* (Hawthorn blossom weevil).....Fam. *Curculionidae*
(See page 1068.)

nenuphar Hbst., *Conotrachelus* (Plum curculio).....Fam. *Curculionidae*
Hosts — Prunus, Pyrus, Malus, Cydonia, Crataegus.
Injury — Larvae feed in fruit, and beetles deform fruits by their feeding punctures.
Distribution — North America east of Rocky Mountains.
Reference — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 243. 1914.

nitidipennis Boh., *Magdalis*.....Fam. *Curculionidae*
Hosts — Crataegus, Populus, Salix.
Distribution — Europe.
References — Redtenbacher, L. Fauna Austriaca. Die Käfer, p. 759. 1858.
Bargagli, P. Rincofori Europei, p. 196. 1883.

oblongus Linn., *Phyllobius*.....Fam. *Curculionidae*
Hosts — Malus, Crataegus, Populus, Corylus, and other species.
Injury — Beetles eat into opening buds, and later eat leaves.
Distribution — Europe, Asia.
Reference — Bargagli, P. Rincofori Europei, p. 79. 1883.
Theobald, F. V. Insect pests of fruits, p. 119. 1909.

olivaceus Gyll., *Rhynchites*.....Fam. *Curculionidae*
Synonym — *Rhynchites comatus* Dej.
Hosts — Crataegus, Corylus, Prunus.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 154, 207. 1872.
Bargagli, P. Rincofori Europei, p. 190. 1883.

pauxillus Germ., *Rhynchites*.....Fam. *Curculionidae*
Hosts — *Crataegus oxyacantha*, Malus.
Injury — Beetles cut off twigs.
Distribution — Europe.

References — Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.
Theobald, F. V. Insect pests of fruits, p. 118. 1909.

politus Say, *Agrilus* ..... Fam. *Buprestidae*
Hosts — Crataegus, Salix, Quercus, Corylus.
Injury — Larva tunnels under bark, causing gall-like swellings on twigs of Crataegus and girdling twigs of oak with a spiral tunnel.
Distribution — North America.
References — Smith, J. B. Insects of New Jersey, p. 295. 1909.
Felt, E. P. New York State Mus. Bul. 200:135. 1918.

pomonae Fabr., *Apion* ..... Fam. *Curculionidae*
Hosts — Vicia, Crataegus.
Distribution — Europe.
References — Curtis, J. Farm insects, p. 487. 1860.
Bargagli, P. Rincofori Europei, p. 165. 1883.

pomorum Linn., *Anthonomus* (Apple blossom weevil) ..... Fam. *Curculionidae*
Hosts — Malus, Pyrus, Crataegus.
Injury — Larva feeds within closed fruit bud, destroying it. Often a very serious pest of apple in Europe. Whitehead records shaking 1530 adults from a single tree in two days.
Distribution — Europe, one specimen recorded from Ohio taken among *A. nebulosus*.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.
Dietz, Wm. G. Amer. Ent. Soc. Trans. 18:204. 1891.
Whitehead, C. Report on injurious insects in Great Britain, p. 44. 1892.
Henschel, G. A. O. Die schädlichen forst- und obstbaum Insekten, p. 571. 1895.
Collinge, W. E. Manual of injurious insects, p. 97. 1912.

posticatus Boh. Schn., *Conotrachelus* ..... Fam. *Curculionidae*
Hosts — Crataegus, Prunus, Carya.
Injury — Larva feeds in fruit.
Distribution — North America.
References — Hamilton, J. Can. ent. 21:34. 1889.
Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 477. 1916.

profundus Lec., *Anthonomus* ..... Fam. *Curculionidae*
Hosts — Crataegus, Quercus.
Injury — Larva feeds in fruit.
Distribution — North America.
Reference — Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 290. 1916.

pruni Ratz., *Eccoptogaster* ..... Fam. *Ipidae*
Hosts — Malus, Pyrus, Prunus, Crataegus, Ulmus.
Injury — Larva girdles weakened trees by mining in cambium layer.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 154. 1872.
Wahl, C. von. Borkenkäfer an den Obstbäumen und ihre Bekämfung. Augustenberg Flugblatt, no. 3, p. 4. 1914.

pruni Linn., *Magdalis* ..... Fam. *Curculionidae*
Hosts — Prunus, Crataegus, Rosa, and other species.
Injury — Larva tunnels under bark of branches.
Distribution — Europe, Asia.

References — Bargagli, P. Rincofori Europei, p. 196. 1883.
Pierce, W. D. Manual of dangerous insects, p. 132. 1917.

pterygomalis Boh., *Polydrusus*.....Fam. *Curculionidae*
Hosts — *Crataegus oxyacantha*, Prunus, Salix, Betula, Corylus, Fagus.
Injury — Beetles feed on foliage.
Distribution — Europe, Asia.
Reference — Pierce, W. D. Journ. econ. ent. 9:431. 19 6.

pubescens Melsh., *Agriotes*.....Fam. *Elateridae*
(See page 1066.)

pubescens Fabr., *Rhynchites*.....Fam. *Curculionidae*
Synonym — *Rhynchites cyanicolor* Schr.
Hosts — Crataegus, Corylus, Alnus, Quercus.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 207. 1872.
Bargagli, P. Rincofori Europei, p. 191. 1883.

quadrigibbus Say, *Tachypterus* (Apple curculio).....Fam. *Curculionidae*
Hosts — Malus, Crataegus, Amelanchier, Pyrus.
Injury — Larva feeds in fruit, beetles puncture fruit and young twigs.
Distribution — Eastern North America.
References — Brooks, F. E. West Virginia Agr. Exp. Sta. Bul. 126. 1910.
Mitchell, J. B., and Pierce, W. D. Ent. Soc. Washington. Proc. 13:53. 1911.

quercata Fabr., *Anthaxia*.....Fam. *Buprestidae*
Hosts — Crataegus, *Pinus strobus*, Cercis, and other species.
Injury — Larva bores in dead or dying branches.
Distribution — North America.
Reference — Knull, Josef N. Ent. news 31:6. 1920.

rufus Ol., *Orchestes*.....Fam. *Curculionidae*
Hosts — Ulmus, Quercus, Salix, Crataegus, Prunus.
Distribution — Europe.
Reference — Bargagli, P. Rincofori Europei, p. 217. 1883.

rugulosus Ratz., *Eccoptogaster* (Fruit-tree bark beetle).....Fam. *Ipidae*
Hosts — Prunus, Cydonia, Malus, Crataegus, Sorbus, Amelanchier.
Injury — Larva and adult mine in cambium layer of weak trees, frequently killing them.
Distribution — Europe, Asia, North America.
References — Gossard, H. A. Ohio Agr. Exp. Sta. Circ. 140. 1913.
Wahl, C. von. Borkenkäfer an den Obstbäumen und ihre Bekämfung. Augustenberg Flugblatt, no. 3, p. 4. 1914.
Swaine, J. M. Can. Agr. Dept. Bul. 14:52. 1918.

scheppardi Kirby, *Choragus*.....Fam. *Anthribidae*
Synonym — *Alticopus galeazii* Vill.
Host — *Crataegus oxyacantha*.
Injury — Larva burrows in dying twigs.
Distribution — Europe.
References — Redtenbacher, L. Fauna Austriaca. Die Käfer, p. 674. 1858.
Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.

sericeus Schal., *Polydrusus*.....Fam. *Curculionidae*
Hosts — Pyrus, Prunus, Crataegus, Malus, Fagus, Salix, Quercus, Alnus, and other species.
Injury — Beetles feed on buds and foliage.

Distribution — Europe, Asia, recently imported into United States (Indiana).
References — Kaltenbach, J. H. Pflanzenfeinde, p. 179. 1872.
Bargagli, P. Rincofori Europei, p. 59. 1883.
Pierce, W. D. Journ. econ. ent. 9:428. 1916.

sericeus Illst., *Rhynchites* ..... Fam. *Curculionidae*
Synonym — *Rhynchites ophthalmicus* Steph.
Hosts — Crataegus, Corylus, Quercus, Betula.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 154, 207. 1872.
Bargagli, P. Rincofori Europei, p. 191. 1883.

sinuatus Oliv., *Agrilus* (Sinuate pear borer) ..... Fam. *Buprestidae*
Hosts — *Pyrus communis*, Crataegus, Sorbus.
Injury — Larva tunnels in sapwood, making a zigzag mine.
Distribution — Europe, North America.
References — Smith, J. B. New Jersey Agr. Exp. Sta. Ann. rept. 15:550. 1894.
Sorauer, P. Handbuch der Pflanzenkrankheiten 3:487. 1913.

subspinosus Fabr., *Macrodactylus* (Rose chafer) ..... Fam. *Scarabaeidae*
Hosts — Vitis, Malus, Pyrus, Rosa, Crataegus, and other species.
Injury — Beetles feed on foliage, flowers, and fruit, and are sometimes very injurious.
Distribution — North America.
References — Hartzell, F. Z. New York (Geneva) Agr. Exp. Sta. Bul. 331:534. 1910.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 397. 1914.

testacea Kirby, *Dichelonycha* ..... Fam. *Scarabaeidae*
(See page 1067.)

tomentosus Fabr., *Byturus* (Raspberry beetle) ..... Fam. *Dermestidae*
Hosts — Rubus, Crataegus, Malus, Pyrus.
Injury — Beetles feed on flowers and foliage.
Distribution — Europe.
References — Sorauer, P. Handbuch der Pflanzenkrankheiten 3:472. 1913.
Bot. journ. London 5:73. 1917.

tubulatus Say, *Idiostethus* ..... Fam. *Curculionidae*
Hosts — Orchids, Crataegus.
Distribution — North America.
References — Pierce, W. D. Nebraska State Bd. Agr. Ann. rept. 1906–07:284. 1907.
Blatchley, W. S., and Leng, C. W. Rhynchophora of north eastern America, p. 404. 1916.

villosula Melsh., *Xanthonia* ..... Fam. *Chrysomelidae*
(See page 1067.)

vittaticollis Rand., *Agrilus* ..... Fam. *Buprestidae*
Hosts — Crataegus, *Prunus virginiana*, Amelanchier.
Injury — Beetles feed on foliage.
Distribution — Eastern United States.
Reference — Blanchard, F. Amer. ent. 5:32. 1889.

Melanotus sp. ..... Fam. *Elateridae*
(See page 1066.)

LEPIDOPTERA

abbotti Swains, *Sphecodina* ..... Fam. *Sphingidae*
Hosts — Vitis, Ampelopsis, *Crataegus tomentosa*.
Injury — Larvae feed on foliage.

Distribution — Eastern North America.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Beutenmueller, William. Hawk moths of the vicinity of New York City, p. 12. 1903.

achatana Fabr., *Olethreutes*.....Fam. *Tortricidae*
Hosts — Crataegus, Malus.
Injury — Larvae roll leaves and eat them.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Theobald, F. V. Insect pests of fruits, p. 81. 1909.

advenella Zk., *Rhodophaea*.....Fam. *Pyralidae*
Hosts — Crataegus, Pyrus.
Injury — Larvae tie leaves and eat them.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, **2**:216. 1910.

aescularia Schiff., *Anisopteryx* (March moth).....Fam. *Geometridae*
Hosts — Crataegus, Malus, Prunus, Pyrus, Quercus, Tilia, Ulmus, Acer, and other species.
Injury — Larvae feed on foliage, sometimes defoliating trees.
Distribution — Europe.
Reference — Theobald, F. V. Insect pests of fruits, p. 61. 1909.

americana Harris, *Acronycta*.....Fam. *Noctuidae*
(See page 1073.)

americana Harris, *Epicnaptera*.....Fam. *Lasiocampidae*
(See page 1075.)

americana Fabr., *Malacosoma* (Apple tent caterpillar).....Fam. *Lasiocampidae*
Hosts — Prunus, Malus, Crataegus, Sorbus, Rosa, Amelanchier, Quercus, Salix, and other species.
Injury — Larvae defoliate branches, living within a silken tent.
Distribution — North America.
References — Felt. E. P. New York State Mus. Memoir 8^2:550. 1906.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 112. 1914.

anatipennella Hüb., *Coleophora*.....Fam. *Elachistidae*
Synonym — *Coleophora tiliella* Zell.
Hosts — Crataegus, Quercus, Tilia, Corylus, *Prunus spinosa*.
Injury — Larva eats patches of green tissue from leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, **2**:400. 1910.

anglicella Stt., *Ornix*.....Fam. *Gracilariidae*
Hosts — Crataegus, Fragaria.
Injury — Larva mines in leaf.
Distribution — Europe, Asia, one record in Massachusetts.
References — Stainton, H. T. Natural history of the Tineina, 8:292. 1864.
Kaltenbach, J. H. Pflanzenfeinde, p. 171. 1872.
Dietz, W. G. Amer. Ent. Soc. Trans. **33**:294. 1907.
Spuler, A. Schmetterlinge Europas, **2**:410. 1910.

angustiorana Haw., *Capua*.....Fam. *Tortricidae*
Hosts — Crataegus, Laurus, Smilax, Pyrus, and other species.

Injury — Larva ties leaves together and feeds on them.
Distribution — Southern Europe, northern Africa, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, **2**:246. 1910.

antiqua Linn., *Notolophus* (Vaporer moth) ..... Fam. *Lymantriidae*
Hosts — Malus, Prunus, Rosa, Crataegus, Ulmus, Tilia, and other species.
Injury — Larvae defoliate branches.
Distribution — Europe, Asia, North America.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Theobald, F. V. Insect pests of fruits, p. 38. 1909.

argyrospila Walk., *Archips* (Fruit-tree leaf roller) ..... Fam. *Tortricidae*
(See page 1077.)

arthemis Dru., *Basilarchia* ..... Fam. *Nymphalidae*
Hosts — Crataegus, Salix, Tilia, Populus.
Injury — Larvae eat leaves, except midrib, beginning at apex.
Distribution — Eastern United States.
References — French, G. H. Butterflies of the eastern United States, p. 208. 1886.
Edwards, H. U. S. Nat. Mus. Bul. 35:27. 1889.

astyanax Fabr., *Basilarchia* ..... Fam. *Nymphalidae*
Hosts — Salix, Prunus, Malus, Tilia, Crataegus, and other species.
Injury — Larva eats leaf on both sides of midrib, beginning at apex.
Distribution — Eastern and southern United States.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 535. 1890.
Holland, W. J. Butterfly book, p. 184. 1898.

aterrima Wck., *Nepticula* ..... Fam. *Nepticulidae*
Host — *Crataegus oxyacantha.*
Injury — Larva mines in leaf.
Distribution — Germany.
Reference — Spuler, A. Schmetterlinge Europas, **2**:480. 1910.

atricollis Stt., *Nepticula* ..... Fam. *Nepticulidae*
Hosts — *Malus malus, Prunus spinosa, Crataegus oxyacantha.*
Injury — Larva mines in leaf.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, **2**:479. 1910.

aurantiaria Esp., *Hibernia* ..... Fam. *Geometridae*
Hosts — Betula, Populus, Rosa, Quercus, Crataegus, and other species.
Injury — Larva eats leaves.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209, 218. 1872.
Spuler, A. Schmetterlinge Europas, **2**:98. 1910.

bajaria Schiff., *Hibernia* ..... Fam. *Geometridae*
Hosts — Prunus, Pyrus, Crataegus, Ligustrum, Syringa.
Injury — Larva eats foliage.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 166. 1872.
Spuler, A. Schmetterlinge Europas, **2**:98. 1910.

betulae Zell., *Lithocolletis* ..... Fam. *Gracilariidae*
Hosts — Crataegus, Pyrus, Cydonia, Betula.
Injury — Larva mines in upper side of leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 198. 1872.
Spuler, A. Schmetterlinge Europas, **2**:419. 1910.

betularia Linn., *Amphidasis* (Pepper-and-salt moth) ..... Fam. *Geometridae*
Hosts — Malus, Prunus, Crataegus, Quercus, Ulmus, Populus, Betula.
Injury — Larvae defoliate trees in late summer.
Distribution — Europe, Asia, Japan.
Reference — Theobald, F. V. Insect pests of fruits, p. 64. 1909.

bidentata Clerck., *Gonodontis* (Scalloped hazel moth) ..... Fam. *Geometridae*
Hosts — Corylus, Betula, Prunus, Crataegus, Pyrus, Quercus, and other species.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia, Japan.
Reference — Collinge, W. E. Manual of injurious insects, p. 138. 1912.

biscutana Wck., *Epiblema* ..... Fam. *Tortricidae*
Hosts — Betula, *Crataegus oxyacantha.*
Injury — Larva ties together terminal clusters of leaves and feeds within.
Distribution — Norway, Finland.
Reference — Spuler, A. Schmetterlinge Europas, **2**:283. 1910.

blandula Hulst., *Catocala* ..... Fam. *Noctuidae*
Host — Crataegus.
Injury — Larvae feed on foliage.
Distribution — Eastern United States, Canada.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 533. 1890.
Smith, J. B. Insects of New Jersey, p. 476. 1909.

brumata Linn., *Cheimatobia* (Winter moth) ..... Fam. *Geometridae*
Hosts — Fruit and forest trees (except conifers) and shrubs.
Injury — Larvae defoliate trees and may attack flowers or fruit.
Distribution — Europe, Asia, Greenland.
References — Ormerod, E. A. Manual of injurious insects, p. 338, 360. 1890.
Theobald, F. V. Insect pests of fruits, p. 50. 1909.
Med. Phytopath. Dienst. Wageningen, no. 3. 1916.

calanus Hüb., *Strymon* (Banded hair-streak) ..... Fam. *Lycaenidae*
Synonym — *Thecla falacer* Godart.
Hosts — Crataegus, Quercus, Hicoria.
Injury — Larva eats holes in leaves.
Distribution — United States and Canada.
References — Scudder, S. Butterflies of New England, **2**:885. 1889.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.

caryae Harris, *Halisidota* (Hickory tussock moth) ..... Fam. *Arctiidae*
Hosts — Hicoria, Juglans, Malus, Cydonia, Crataegus, and other species.
Injury — Larvae eat foliage.
Distribution — United States east of Rocky Mountains.
Reference — Soule, Caroline G. Psyche **6**:158. 1891.

catax Linn., *Eriogaster* ..... Fam. *Lasiocampidae*
Hosts — Crataegus, Quercus, Populus, Betula.
Injury — Larvae defoliate branches, which they cover with silken tents.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, **1**:117. 1908.

cecropia Linn., *Platysamia* ..... Fam. *Saturniidae*
Hosts — Crataegus, Malus, Pyrus, Prunus, Salix, Acer, Syringa, and other species.
Injury — Larva eats leaves.
Distribution — North America east of Rocky Mountains.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Dickerson, Mary C. Moths and butterflies, p. 157. 1901.

cerisolella Pey., *Lithocolletis* ..... Fam. *Gracilariidae*
Hosts — Crataegus, *Sorbus torminalis*.
Injury — Larva mines in leaf on under side.
Distribution — Southern France.
Reference — Spuler, A. Schmetterlinge Europas, 2:415. 1910.

chionosema Zell., *Olethreutes* ..... Fam. *Tortricidae*
(See page 1077.)

chrysorrhea Linn., *Euproctis* (Brown-tail moth) ..... Fam. *Lymantriidae*
Hosts — Crataegus and most other deciduous trees.
Injury — Larvae defoliate trees.
Distribution — Europe, Asia Minor, New England States.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1:132. 1908.

clerkella Linn., *Lyonetia* ..... Fam. *Lyonetiidae*
Hosts — Pyrus, Prunus, Crataegus, Sorbus, Betula.
Injury — Larva makes serpentine mine in leaf.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, 2:422. 1910.

coeruleocephala Linn., *Diloba* (Figure-8 moth) ..... Fam. *Noctuidae*
Hosts — Malus, Prunus, Crataegus, and other species.
Injury — Larva eats foliage, sometimes defoliating hawthorn hedges.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Theobald, F. V. Insect pests of fruits, p. 35. 1909.

cognataria Guen., *Lycia* ..... Fam. *Geometridae*
(See page 1076.)

cognatellus Hüb., *Yponomeuta* (Hedge ermine moth) ..... Fam. *Yponomeutidae*
Hosts — *Crataegus oxyacantha*, Euonymus.
Injury — Larva eats leaves, sometimes stripping hedges.
Distribution — Europe.
References — Spuler, A. Schmetterlinge Europas, 2:444. 1910.
Noel, P. Jardinage 4:363. 1914.

concinna A. and S., *Schizura* (Red-humped apple caterpillar) ..... Fam. *Notodontidae*
Hosts — Malus, Crataegus, Prunus, Pyrus, and other species.
Injury — Larvae defoliate branches, feeding in a colony.
Distribution — North America.
References — Saunders, William. Can. ent. 13:139. 1 81.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 125. 1914.

concomitella Bnks., *Lithocolletis* ..... Fam. *Gracilariidae*
Synonym — *Lithocolletis pomifoliella* Zell.
Hosts — Malus, Crataegus.
Injury — Larva mines in leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 198. 1872.
Spuler, A. Schmetterlinge Europas, 2:415. 1910.

congelatella Clerck., *Exapate* ..... Fam. *Tortricidae*
Hosts — Crataegus, Sorbus, Prunus, Pyrus, Rubus, Berberis, Ligustrum, and other species.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe.

References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, 2:254. 1910.

contaminana Hüb., *Acalla*.....Fam. *Tortricidae*
Hosts — Crataegus, Prunus, Pyrus, Malus, Quercus, and other species.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, 2:245. 1910.

corylifoliella Haw., *Lithocolletis*.....Fam. *Gracilariidae*
Hosts — Crataegus, Pyrus, Malus, Sorbus.
Injury — Larva mines in leaf.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, 2:417. 1910.

crataegana Hüb., *Cacoecia*.....Fam. *Tortricidae*
Synonym — *Penthina robrana* Schiff.
Hosts — Crataegus, Quercus, Betula, Populus, Malus, Cotoneaster, and other species.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, 2:247. 1910.

crataegella Clem., *Lithocolletis*.....Fam. *Gracilariidae*
Hosts — Crataegus, Pyrus, *Prunus serotina*.
Injury — Larva mines in leaf.
Distribution — North America.
References — Braun, A. F. Amer. Ent. Soc. Trans. 34:301. 1908.
Wilson, H. F. Oregon Agr. Exp. Sta. Bien. crop pest and hort. rept. 2:119. 1915.

crataegella Linn., *Scythropia*.....Fam. *Yponomeutidae*
Hosts — *Crataegus oxyacantha*, *Prunus spinosa*, Pyrus.
Injury — Larva spins a tent over the branch and eats the leaves within it.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 169. 1872.
Spuler, A. Schmetterlinge Europas, 2:443. 1910.

crataegi Linn., *Aporia* (Fruit-tree pierid).....Fam. *Pieridae*
Hosts — Crataegus, Pyrus, Malus, Prunus, Sorbus, Salix, Quercus, and other species.
Injury — Larva eats foliage, often stripping trees.
Distribution — Europe.
References — Bechstein, J. M., and Scharfenberg, G. L. Naturgeschichte der schädlichen Forstinsekten, p. 303. 1805.
Sasscer, E. R. Journ. econ. ent. 11:126. 1918.

crataegi Zell., *Bucculatrix*.....Fam. *Lyonetiidae*
Host — Crataegus.
Injury — Larva mines in leaf and later feeds externally on leaf.
Distribution — Europe.
Reference — Stainton, H. T. Natural history of the Tineina, 7:68. 1862.

crataegi Saund., *Catocala*.....Fam. *Noctuidae*
Host — Crataegus.
Injury — Larva feeds on foliage.
Distribution — Eastern North America.
References — Saunders, William. Can. ent. 8:72. 1876.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 532. 1890.

crataegi Linn., *Trichiura* ..... Fam. *Lasiocampidae*
Hosts — Prunus, Crataegus, Corylus, Betula, Salix, Alnus.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 1:114. 1908.

crataegifoliella Clem., *Nepticula* ..... Fam. *Nepticulidae*
Host — *Crataegus uniflora.*
Injury — Larva mines in leaf.
Distribution — Eastern United States.
Reference — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 534. 1890.

crataegifoliella Clem., *Ornix* ..... Fam. *Gracilariidae*
Host — *Crataegus tomentosa.*
Injury — Larva mines in leaf.
Distribution — Eastern United States.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 534. 1890.
Dietz, W. G. Amer. Ent. Soc. Trans. *33*:292. 1907.

cuculla Esp., *Lophopteryx* ..... Fam. *Notodontidae*
Synonym — *Notodonta cucullina* Hüb.
Hosts — *Acer campestre*, Crataegus.
Injury — Larva feeds on foliage.
Distribution — Europe.
Reference — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.

cucullatella Linn., *Nola* ..... Fam. *Nolidae*
Synonym — *Hercyna palliolalis* Hüb.
Hosts — Prunus, Malus, Crataegus.
Injury — Larva eats foliage.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, *2*:122. 1910.

curvilineella Chamb., *Blastodacna* (Hawthorn fruit miner) ..... Fam. *Cosmopterygidae*
(See page 1080.)

dactylina Grote, *Acronycta* ..... Fam. *Noctuidae*
(See page 1073.)

defoliaria Linn., *Hibernia* (Mottled umber moth) ..... Fam. *Geometridae*
Hosts — Malus, Prunus, Betula, Corylus, Quercus, Crataegus, Pyrus, and other species.
Injury — Larvae defoliate trees.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 163. 1872.
Theobald, F. V. Insect pests of fruits, p. 58. 1909.

dispar Linn., *Lymantria* (Gipsy moth) ..... Fam. *Lymantriidae*
Hosts — Species a very general feeder on trees. Crataegus a favored food plant.
Injury — Larvae defoliate trees.
Distribution — Europe, Asia, New England States.
References — Spuler, A. Schmetterlinge Europas, 1:131. 1908.
Mosher, F. H. U. S. Agr. Dept. Bul. 250. 1915.

disstria Hüb., *Malacosoma* (Forest tent caterpillar) ..... Fam. *Lasiocampidae*
Hosts — Acer, Quercus, Crataegus, Malus, and other species.
Injury — Larvae defoliate branches, feeding in colonies.
Distribution — North America.

References — Insect life **3**:478. 1890.
Insect life **4**:75. 1891.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 119. 1914.

dubitata Linn., *Triphosa*.....Fam. *Geometridae*
Hosts — Crataegus, Prunus, Rhamnus.
Injury — Larva webs leaves together and feeds on them.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 166. 1872.
Spuler, A. Schmetterlinge Europas, **2**:36. 1910.

ephemeraeformis Haw., *Thyridopteryx* (Common bagworm).....Fam. *Psychidae*
Hosts — Species a very general feeder on trees and shrubs, including Crataegus.
Injury — Larva defoliates trees.
Distribution — North America east of Rocky Mountains.
Reference — Beutenmueller, William. Ent. Amer. **3**:157. 1887.

ephippella Fabr., *Argyresthia*.....Fam. *Yponomeutidae*
Synonym — *Argyresthia pruniella* Linn.
Hosts — Crataegus, Pyrus, Prunus, Sorbus, Corylus.
Injury — Larva eats leaf and blossom buds.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, **2**:447. 1910.

euphorbiae Fabr., *Acronycta*.....Fam. *Noctuidae*
Hosts — Species a general feeder on trees, including Crataegus.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, **1**:139. 1908.

fabriciana Linn., *Simaethis*.....Fam. *Glyphipterygidae*
Synonyms — *Tinea oxyacanthella* Linn., *Crambus oxyacanthae* Fabr.
Hosts — Urtica, Parietaria, Symphytum, Crataegus.
Injury — Larva feeds in leaf roll.
Distribution — Europe.
References — Bechstein, J. M., and Scharfenberg, G. L. Naturgeschichte der schädlichen Forstinsekten, p. 805. 1805.
Spuler, A. Schmetterlinge Europas, **2**:297. 1910.

fasciellus Hüb., *Holcophora*.....Fam. *Gelechiidae*
Hosts — Prunus, Crataegus.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, **2**:354. 1910.

fletcherella Fern., *Coleophora* (Cigar case-bearer).....Fam. *Elachistidae*
Hosts — Malus, Crataegus, Pyrus, Cydonia.
Injury — Larva eats holes into leaf and makes a small blotch mine around each hole.
Distribution — North America.
References — Hammar, A. G. U. S. Ent. Bur. Bul. 80:33. 1909.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 47. 1914.

fulminea Scop., *Catocala*.....Fam. *Noctuidae*
Synonym — *Catocala paranympha* Linn.
Hosts — Crataegus, Prunus, Pyrus, Quercus.
Injury — Larva eats foliage.

Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1:317. 1908.

geminatella Pack., *Ornix* (Unspotted tentiform leaf miner of apple) ..... Fam. *Gracilariidae*
Synonym — *Lithocolletis prunivorella* Chamb.
Hosts — Crataegus, Pyrus, Prunus.
Injury — Larva mines in leaf.
Distribution — Eastern United States.
Reference — Haseman, L. Journ. agr. res. 6:289. 1916.

glaucatus Schiff., *Cilex* ..... Fam. *Drepanidae*
Hosts — Prunus, Crataegus.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia.
References Kaltenbach, J. H. Pflanzenfeinde, p. 208. 187 .
Spuler, A. Schmetterlinge Europas, 1:107. 1908.

gothica Linn., *Taeniocampa* ..... Fam. *Noctuidae*
Hosts — Crataegus, Tilia, Quercus, and other species.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1:239. 1908.

gratiosella Stt., *Nepticula* ..... Fam. *Nepticulidae*
Host — *Crataegus oxyacantha.*
Injury — Larva mines in leaf.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, 2:476. 1910.

grotiana T., *Dichelia* ..... Fam. *Tortricidae*
Hosts — Crataegus, Quercus, Ulmus, Rubus, and other species.
Injury — Larva ties leaves and feeds on them.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2:246. 1910.

hellerella Dup., *Blastodacna* ..... Fam. *Cosmopterygidae*
Hosts — Crataegus, Malus, Pyrus.
Injury — Larva tunnels in fruit of Crataegus and in fruit spurs and buds of apple.
Distribution — Europe.
References — Theobald, F. V. Insect pests of fruits, p. 92. 1909.
Spuler, A. Schmetterlinge Europas, 2:387. 1910.

hemerobiella Scop., *Coleophora* ..... Fam. *Elachistidae*
Hosts — Crataegus, Pyrus, Prunus.
Injury — Larva eats star-shaped area from under side of leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, 2:400. 1910.

heparana Schiff., *Pandemis* ..... Fam. *Tortricidae*
Hosts — Crataegus, Prunus, Sorbus, Malus, Alnus, Betula, Fagus, and other species.
Injury — Larva rolls leaf and feeds within the roll.
Distribution — Europe, Japan.
Reference — Spuler, A. Schmetterlinge Europas, 2:249. 1910.

holmiana Linn., *Acalla* ..... Fam. *Tortricidae*
Hosts — Crataegus, Rosa, Prunus, Malus, Pyrus, Quercus.

Injury — Larva ties leaves together and feeds on them.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, **2**:244. 1910.

ignobilella Stt., *Nepticula* ..... Fam. *Nepticulidae*
Host — *Crataegus oxyacantha.*
Injury — Larva mines in leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 211. 1872.
Spuler, A. Schmetterlinge Europas, **2**:477. 1910.

incerta Hufn., *Taeniocampa* ..... Fam. *Noctuidae*
Synonym — *Taeniocampa instabilis* Hüb.
Hosts — Crataegus, Salix, Prunus, Quercus, Malus, and other species.
Injury — Larva eats leaves, and sometimes eats holes in apple fruit.
Distribution — Europe, Asia, South America.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Theobald, F. V. Insect pests of fruits, p. 66. 1909.

indigenella Zell., *Mineola* (Leaf crumpler) ..... Fam. *Pyralidae*
Synonyms — *Acrobasis nebulella* Riley, *Phycita nebulo* Walsh.
Hosts — Malus, Crataegus, *Hicoria pecan*, and other species.
Injury — Larva feeds on leaves, living in a case composed of leaf particles and silk.
Distribution — North America.
Reference — Riley, C. V. Fourth Missouri report, p. 42. 1872.

integerrima G. and R., *Datana* (Black-walnut caterpillar) ..... Fam. *Notodontidae*
Hosts — Juglans, Hicoria, Malus, Crataegus, and other species.
Injury — Larvae defoliate branches, feeding in a colony.
Distribution — Eastern United States.
Reference — Packard, A. S. Nat. Acad. Sci. Memoir 1:120. 1895.

inusitatumella Chamb., *Ornix* ..... Fam. *Gracilariidae*
Host — Crataegus.
Injury — Larva mines in upper surface of leaf.
Distribution — Eastern United States.
References — Chambers, V. T. Can. ent. **5**:48. 1873.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.

io Fabr., *Automeris* ..... Fam. *Saturniidae*
(See page 1073.)

janthinana Dup., *Grapholitha* ..... Fam. *Tortricidae*
Synonym — *Tortrix incisana* Schiff.
Host — Crataegus.
Injury — Larva tunnels in fruit, then in twigs.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, **2**:294. 1910.

lacustrata Guen., *Mesoleuca* ..... Fam. *Geometridae*
Hosts — Rubus, Betula, Crataegus, Salix.
Injury — Larva feeds on foliage.
Distribution — Northeastern North America, Europe.
References — Packard, A. S. A monograph of the geometrid moths of the United States, p. 158. 1876.
Smith, J. B. Insects of New Jersey, p. 497. 1909.

lanestris Linn., *Eriogaster* ..... Fam. *Lasiocampidae*
Hosts — Prunus, Crataegus, Betula, Tilia, Salix.

Injury — Larvae defoliate branches, feeding gregariously in a white tent of silk.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1:117. 1908.

leucatella Clerck., *Recurvaria* ..... Fam. *Gelechiidae*
Hosts — Crataegus, Pyrus, Prunus, Sorbus.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, 2:356. 1910.

leucophaearia Schiff., *Hibernia* ..... Fam. *Geometridae*
Hosts — Quercus, Crataegus, Prunus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia, Japan.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, 2:98. 1910.

leucostigma A. and S., *Hemerocampa* (White-marked tussock caterpillar) .. Fam. *Lymantriidae*
(See page 1075.)

limbata Haw., *Nematocampa* ..... Fam. *Geometridae*
Synonym — *Nematocampa filamentaria* Guen.
Hosts — Crataegus, Fragaria.
Injury — Larva eats foliage.
Distribution — North America.
References — Packard, A. S. A monograph of the geometrid moths of the United States, p. 471. 1876.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.

parops Bdv. and Lec., *Strymon* (Striped hair-streak) ..... Fam. *Lycaenidae*
Hosts — Malus, Crataegus, Prunus, Amelanchier, Salix, Quercus, and other species.
Injury — Larva eats entire leaf and sometimes bores into fruit.
Distribution — United States, Canada.
References — Scudder, S. Butterflies of New England, 2:877. 1889.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.

ludifica Linn., *Trichosea* ..... Fam. *Noctuidae*
Hosts — Sorbus, Crataegus, Malus.
Injury — Larva eats leaves.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, 1:135. 1908.

lunaria Schiff., *Selenia* ..... Fam. *Geometridae*
Hosts — Malus, Prunus, Crataegus, and other species.
Injury — Larva eats leaves.
Distribution — Europe, Asia.
Reference — Kaltenbach, J. H. Pflanzenfeinde, p. 165. 1872.

lutarea Haw., *Swammerdamia* ..... Fam. *Yponomeutidae*
Synonym — *Swammerdamia oxyacanthella* Dup.
Hosts — Crataegus, Sorbus.
Injury — Larva eats parenchymous tissue of leaves, which it ties together.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210, 782. 1872.
Spuler, A. Schmetterlinge Europas, 2:445. 1910.

luteicoma G. and R., *Acronycta*.....Fam. *Noctuidae*
(See page 1073.)

luteolata Linn., *Opisthograptis*.....Fam. *Geometridae*
Synonym — *Rumia crataegata* Linn.
Hosts — Crataegus, Prunus, Malus, Pyrus, Sorbus.
Injury — Larva eats foliage.
Distribution — Europe, Asia, northern Africa.
Reference — Kaltenbach, J. H. Pflanzenfeinde, p. 165. 1872.

magnarius Güen., *Ennomos*.....Fam. *Geometridae*
(See page 1076.)

malifoliella Clem., *Tischeria* (Apple trumpet leaf-miner).....Fam. *Gracilariidae*
Hosts — Malus, Crataegus.
Injury — Larva mines in upper side of leaf, widening the mine gradually as it grows.
Distribution — North America.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Quaintance, A. L. U. S. Ent. Bur. Bul. 68:23. 1908.

malimalifoliella Braun, *Lithocolletis* (Spotted tentiform leaf miner of apple).Fam. *Gracilariidae*
Hosts — Malus, Cydonia, *Crataegus mollis*.
Injury — Larva mines in under side of leaf.
Distribution — Eastern United States.
Reference — Braun, A. F. Amer. Ent. Soc. Trans. 34:300. 1908.

malivorella Riley, *Coleophora* (Pistol case-bearer).....Fam. *Elachistidae*
(See page 1079.)

manteo Doub., *Heterocampa*.....Fam. *Notodontidae*
(See page 1074.)

marginaria Borckh., *Hibernia*.....Fam. *Geometridae*
Hosts — Crataegus, Betula, Quercus, Tilia, Populus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Spuler, A. Schmetterlinge Europas, 2:99. 1910.
Pierce, W. D. Manual of dangerous insects, p. 132. 1917.

melinus Hüb., *Strymon* (Common hair-streak).....Fam. *Lycaenidae*
Hosts — Hops, beans, Crataegus, and other species.
Injury — Larva eats leaves and sometimes bores into fruit.
Distribution — North America, Central America.
References — Scudder, S. Butterflies of New England, 2:850. 1889.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 535. 1890.
Crosby, C. R., and Leonard, M. D. Manual of vegetable garden insects, p. 84. 1918.

ministra Dru., *Datana* (Yellow-necked apple caterpillar).....Fam. *Notodontidae*
(See page 1075.)

myopiforme Bkh., *Trochilium*.....Fam. *Sesiidae*
Hosts — *Malus malus*, *Pyrus communis*, *Prunus domestica*, Crataegus.
Injury — Larva tunnels under bark of unhealthy trees.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2:310. 1910.

myops A. and S., *Paonias*.....Fam. *Sphingidae*
Hosts — Prunus, Crataegus, Salix, Corylus, and other species.
Injury — Larva eats leaves.

Distribution — Eastern United States.
Reference — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 525, 536. 1890.

naevana Hüb., *Rhopobota* ..... Fam. *Tortricidae*
Hosts — Prunus, Crataegus, Malus, Rhamnus, Sorbus, Ilex, and other species.
Injury — Larva eats leaves of new shoots and ties them together.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, **2**:273. 1910.

nanella Hüb., *Recurvaria* (Lesser apple bud moth) ..... Fam. *Gelechiidae*
Synonym — *Recurvaria crataegella* Busck.
Hosts — Crataegus, Malus, Pyrus, Prunus.
Injury — Larvae destroy opening buds, and mine in leaves in late summer.
Distribution — Europe, North America.
References — Scott, E. W., and Paine, J. H. U. S. Agr. Dept. Bul. 113. 1914.
Sanders, G. E., and Dustan, A. G. Canada Agr. Dept., Ent. Branch Bul. 16:33. 1919.

neustria Linn., *Malacosoma* (Lackey moth) ..... Fam. *Lasiocampidae*
Hosts — Malus, Pyrus, Prunus, Crataegus, Populus, Betula, Quercus, and other species
Injury — Larva eats leaves, frequently defoliating fruit trees, and builds silken tent over colony.
Distribution — Europe, Asia.
References — Spuler, A. Schmetterlinge Europas, **1**:115. 1908.
Theobald, F. V. Insect pests of fruits, p. 30. 1909.

nitidella Fabr., *Argyresthia* (Cherry fruit moth) ..... Fam. *Yponomeutidae*
Hosts — Prunus, Crataegus.
Injury — Larva destroys young shoots of hawthorn, and bores into cherry fruit.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 211. 1872.
Theobald, F. V. Insect pests of fruits, p. 192. 1909.
Spuler, A. Schmetterlinge Europas, **2**:447. 1910.

nitidella Hein., *Nepticula* ..... Fam. *Nepticulidae*
Host — *Crataegus oxyacantha.*
Injury — Larva mines in leaf.
Distribution — Southwestern Germany.
Reference — Spuler, A. Schmetterlinge Europas, **2**:474. 1910.

nubeculana Clem., *Ancylis* ..... Fam. *Tortricidae*
(See page 1077.)

nubilana Hüb., *Cnephasia* ..... Fam. *Tortricidae*
Hosts — Crataegus, Pyrus, Prunus, Malus, Betula.
Injury — Larva feeds between leaves tied together with silk.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, **2**:253. 1910.

occidentalis G. and R., *Acronycta* ..... Fam. *Noctuidae*
(See page 1074.)

ocellana Fabr., *Tmetocera* (Bud moth) ..... Fam. *Tortricidae*
Hosts — Crataegus, Sorbus, Malus, Pyrus, Cydonia, Prunus, Rubus, and other species
Injury — Larva destroys buds in early spring, and later ties the leaves together and feeds on them.
Distribution — Europe, North America.

References — Kaltenbach, J. H. Pflanzenfeinde, p. 192. 1872.
Slingerland, M. V. Cornell Univ. Agr. Exp. Sta. Bul. 107. 1896.
Theobald, F. V. Insect pests of fruits, p. 82. 1909.

oleagina Fabr., *Valeria* ..... Fam. *Noctuidae*
Hosts — Crataegus, Prunus.
Injury — Larva feeds on foliage at night.
Distribution — Southern Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 1:185. 1908.

oreasella Clem., *Argyresthia* ..... Fam. *Yponomeutidae*
(See page 1078.)

oxyacanthae Frey, *Lithocolletis* ..... Fam. *Gracilariidae*
Host — *Crataegus oxyacantha.*
Injury — Larva mines in under side of leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 211. 1872.
Spuler, A. Schmetterlinge Europas, *2*:415. 1910.

oxyacanthae Linn., *Miselia* ..... Fam. *Noctuidae*
Host — *Crataegus oxyacantha.*
Injury — Larva eats foliage at night.
Distribution — Europe, Asia Minor.
References — Bechstein, J. M., and Scharfenberg, G. L. Naturgeschichte der schädlichen Forstinsekten, p. 504. 1805.
Spuler, A. Schmetterlinge Europas, 1:204. 1908.

oxyacanthella Stt., *Nepticula* ..... Fam. *Nepticulidae*
Hosts — *Crataegus oxyacantha*, *Malus malus*, Sorbus.
Injury — Larva mines in leaf on upper side.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 199. 1872.
Spuler, A. Schmetterlinge Europas, *2*:474. 1910.

padellus Linn., *Yponomeuta* (Hawthorn ermine moth) ..... Fam. *Yponomeutidae*
Synonym — *Hyponomeuta padella* Linn.
Hosts — Crataegus, Prunus, Vitis.
Injury — Larvae mine in leaves while young, then skeletonize leaves while living colonially in tents.
Distribution — Europe, North America (recently imported).
References — Theobald, F. V. Insect pests of fruits, p. 86. 1909.
Parrott, P. J. Journ. econ. ent. 11:55. 1918.

pariana Clerck., *Simaethis* ..... Fam. *Glyphipterygidae*
Hosts — Malus, Sorbus, Crataegus, Betula, Prunus.
Injury — Larva makes a slight web over the leaf, then skeletonizes it.
Distribution — Europe, Asia Minor, North America (recently imported).
References — Spuler, A. Schmetterlinge Europas, *2*:297. 1910.
Felt, E. P. New York State Mus. Bul. 202:33. 1917.

pedaria Fabr., *Phigalia* ..... Fam. *Geometridae*
Hosts — Pyrus, Quercus, Betula, Prunus, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 164. 1872.
Spuler, A. Schmetterlinge Europas, *2*:100. 1910.

podalirius Linn., *Papilio*.....Fam. *Papilionidae*
Hosts — Crataegus, Sorbus, Prunus, Amygdalus.
Injury — Larva eats foliage.
Distribution — Southern and central Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 1:2. 1908.

polygama Guen., *Catocala*.....Fam. *Noctuidae*
Host — Crataegus.
Injury — Larva feeds on foliage.
Distribution — Eastern North America.
References — Saunders, William. Can. ent. 8:72. 1876.
Edwards, H. U. S. Nat. Mus. Bul. 35:97. 1889.

polyphemus Cram., *Telea*.....Fam. *Saturniidae*
Hosts — Quercus, Ulmus, Juglans, Hicoria, Tilia, Betula, Rosa, Crataegus, and others.
Injury — Larva feeds on foliage.
Distribution — North America.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Dickerson, Mary C. Moths and butterflies, p. 169. 1901.

pometeria Peck, *Alsophila* (Fall cankerworm).....Fam. *Geometridae*
(See page 1076.)

pomifoliella Clem., *Bucculatrix* (Ribbed-cocoon-maker of apple).....Fam. *Lyonetiidae*
(See page 1079.)

pomonella Linn., *Cydia* (Codling moth).....Fam. *Tortricidae*
Hosts — Malus, Pyrus, Cydonia; occasionally Crataegus, Rosa, Prunus, *Juglans regia*.
Injury — Larva bores in fruit.
Distribution — Europe, Asia, North America, Africa, Australia.
References — Bruner, L. Nebraska State Hort. Soc. Rept. 1894:216. 1894.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 10. 1914.

populi Linn., *Poecilocampa*.....Fam. *Lasiocampidae*
Hosts — Populus, Tilia, Quercus, Ulmus, Betula, Salix, Crataegus, Malus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Theobald, F. V. Insect pests of fruits, p. 34. 1909.

porrinata Zell., *Nemoria*.....Fam. *Geometridae*
Hosts — Corylus, Crataegus, and other species.
Injury — Larva eats leaves.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 2:4. 1910.

praefica Grote, *Prodenia* (Yellow-striped army worm).....Fam. *Noctuidae*
Hosts — *Medicago sativa*, Vitis, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — Pacific coast of the United States.
References — Essig, E. O. Injurious and beneficial insects of California, p. 401. 1915.
Crosby, C. R., and Leonard, M. D. Manual of vegetable garden insects, p. 295. 1918.

prunetorum Stt., *Nepticula*.....Fam. *Nepticulidae*
Hosts — Prunus, Crataegus.
Injury — Larva mines in leaf.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2:476. 1910.

pruniana Hüb., *Argyroploce*.....Fam. *Tortricidae*
Hosts — Prunus, Sorbus, Rosa, Salix, Crataegus.
Injury — Larva ties leaves together and feeds on them.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2:265. 1910.

prunivora Walsh, *Laspeyresia* (Lesser apple worm).....Fam. *Tortricidae*
Hosts — Crataegus, Malus, Prunus.
Injury — Larva bores in fruit.
Distribution — North America east of Rocky Mountains.
Reference — Quaintance, A. L. U. S. Ent. Bur. Bul. 68:49. 1908.

psi Linn., *Acronycta* (Dagger moth).....Fam. *Noctuidae*
Hosts — Malus, Prunus, Crataegus, Salix, Rosa, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia, Japan.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Theobald, F. V. Insect pests of fruits, p. 41. 1909.

pudibunda Linn., *Dasychira* (Red-tail moth).....Fam. *Lymantriidae*
Hosts — Species a general feeder on fruit and forest trees. Crataegus a favored food plant.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Spuler, A. Schmetterlinge Europas, 1:129. 1908.
Sorauer, P. Handbuch der Pflanzenkrankheiten, 3:384. 1913.

purpuralis Linn., *Pyrausta*.....Fam. *Pyralidae*
Hosts — Mentha, Nepeta, Plantago, Crataegus.
Injury — Larva feeds on leaves spun together with silk.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, 2:236. 1910.

pygmaeella Haw., *Nepticula*.....Fam. *Nepticulidae*
Hosts — *Crataegus oxyacantha*, *Malus malus*.
Injury — Larva mines in leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 199. 1872.
Spuler, A. Schmetterlinge Europas, 2:473. 1910.

pyramidea Linn., *Amphipyra*.....Fam. *Noctuidae*
Hosts — Crataegus and many other trees.
Injury — Larva eats foliage.
Distribution — Europe, Asia, East Indies.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1:238. 1908.

pyramidoides Guen., *Amphipyra*.....Fam. *Noctuidae*
Hosts — Crataegus and many other trees.
Injury — Larva eats foliage.
Distribution — North America.
Reference — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 171, 536. 1890.

pyri Harris, *Aegeria* (Pear borer) ..... Fam. *Sesiidae*
Synonym — *Sesia pyri* Boisd.
Hosts — Pyrus, Malus, Crataegus, Amelanchier, Prunus.
Injury — Larva burrows in bark and sapwood.
Distribution — Eastern United States.
Reference — Brooks, F. E. U. S. Agr. Dept. Bul. 887. 1920.

pyrina Linn., *Zeuzera* (Leopard moth) ..... Fam. *Cossidae*
Synonym — *Zeuzera aesculi* Linn.
Hosts — Pyrus, Malus, Prunus, Crataegus, Fraxinus, Populus, Betula, Ulmus, and other species.
Injury — Larva mines in solid healthy wood of branches.
Distribution — Europe, Asia, Japan, North America.
References — Lintner, A. J. Ninth report on injurious insects of New York, p. 426. 1893.
Theobald, F. V. Insect pests of fruits, p. 46. 1909.

quadrifasciana Fern., *Eulia* ..... Fam. *Tortricidae*
(See page 1078.)

quercifolia Linn., *Gastropacha* (Lappet moth) ..... Fam. *Lasiocampidae*
Hosts — Malus, Pyrus, Prunus, Crataegus, Quercus, and other species.
Injury — Larvae defoliate branches, especially of nursery trees, in spring.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1:122. 1908.
Collinge, W. E. Manual of injurious insects, p. 137. 1912.

quercus Linn., *Lasiocampa* ..... Fam. *Lasiocampidae*
Hosts — Crataegus, Quercus, Betula, Salix, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1:118. 1908.

quernaria A. and S., *Nacophora* ..... Fam. *Geometridae*
Hosts — Quercus, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — Eastern North America.
References — Packard, A. S. A monograph of the geometrid moths of the United States, p. 411. 1876.
Edwards, H. U. S. Nat. Mus. Bul. 35:106. 1889.

radcliffei Harv., *Acronycta* ..... Fam. *Noctuidae*
(See page 1074.)

regiella H. S., *Nepticula* ..... Fam. *Nepticulidae*
Host — *Crataegus oxyacantha.*
Injury — Larva mines in leaf.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 211. 1872.
Spuler, A. Schmetterlinge Europas, 2:475. 1910.

rhediella Clerck., *Pamene* ..... Fam. *Tortricidae*
Hosts — Crataegus, Malus, Prunus, Cornus.
Injury — Larva feeds in fruit of Crataegus and also eats leaves.
Distribution — Europe, Asia Minor.
References — Theobald, F. V. Insect pests of fruits, p. 80. 1909.
Spuler, A. Schmetterlinge Europas, 2:296. 1910.

ribeana Hüb., *Pandemis*.....Fam. *Tortricidae*
Hosts — Crataegus, Rosa, Prunus, Malus, Pyrus, Quercus, Sorbus, and other species.
Injury — Larva ties several leaves together and feeds within.
Distribution — Europe, Asia, Japan, East Indies.
Reference — Spuler, A. Schmetterlinge Europas, 2:249. 1910.

rosaceana Harris, *Cacoecia* (Oblique-banded leaf roller).....Fam. *Tortricidae*
Hosts — Crataegus, Malus.
Injury — Larvae tie leaves together and feed on them.
Distribution — North America.
References — Essig, E. O. Injurious and beneficial insects of California, p. 441. 1915.
Sanders, G. E., and Dustan, A. G. Canada Agr. Dept., Ent. Branch. Bul. 16:30. 1919.

rosana Linn., *Cacoecia*.....Fam. *Tortricidae*
Synonym — *Tortrix laevigana* Schiff.
Hosts — Malus, Crataegus, Pyrus, Prunus, and other species.
Injury — Larvae tie leaves together and feed on them.
Distribution — Europe, Asia Minor, North America.
References — Theobald, F. V. Insect pests of fruits, p. 80. 1909.
Sorauer, P. Handbuch der Pflanzenkrankheiten, 3:299. 1913.

scintillans Braun, *Nepticula*.....Fam. *Nepticulidae*
Host — *Crataegus mollis*.
Injury — Larva mines in leaf.
Distribution — Ohio.
Reference — Braun, A. F. Amer. Ent. Soc. Trans. 43:167. 1917.

scitella Zell., *Cemiostoma* (Pear leaf blister moth).....Fam. *Lyonetiidae*
Hosts — Crataegus, Pyrus, Prunus, Sorbus.
Injury — Larva mines in leaf.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 197. 1872.
Theobald, F. V. Insect pests of fruits, p. 330. 1909.
Spuler, A. Schmetterlinge Europas, 2:223. 1910.

scitula Harris, *Sesia*.....Fam. *Sesiidae*
(See page 1076.)

selenana Guen., *Ancylis*.....Fam. *Tortricidae*
Hosts — Pyrus, Malus, Crataegus.
Injury — Larva ties leaves together and feeds within.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2:270. 1910.

signatana Dgl., *Steganoptycha*.....Fam. *Tortricidae*
Synonym — *Grapholitha kroesmanniana* Hein.
Hosts — Prunus, Crataegus.
Injury — Larva eats young terminal leaves after tying them with silk.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, 2:276. 1910.

similis Fuessl., *Porthesia* (Gold-tail moth).....Fam. *Lymantriidae*
Synonym — *Liparis auriflua* Hüb.
Hosts — Crataegus and most other fruit and non-coniferous forest trees.
Injury — Larva eats foliage.
Distribution — Europe.

References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1:133. 1908.

sphinx Hufn., *Brachionycha* ..... Fam. *Noctuidae*
Synonym — *Asteroscopus cassinia* S. V.
Hosts — Quercus, Populus, Malus, Prunus, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, 1:203. 1908.

spiniana Dup., *Pamene* ..... Fam. *Tortricidae*
Hosts — Crataegus, Prunus, Alnus.
Injury — Larva feeds in blossom, destroying it.
Distribution — Europe, northern Africa.
Reference — Spuler, A. Schmetterlinge Europas, 2:295. 1910.

splendoriferella Clem., *Coptodisca* (Resplendent shield-bearer) ..... Fam. *Elachistidae*
Hosts — Malus, Crataegus, *Prunus serotina*, Pyrus, Cydonia.
Injury — Larva mines in leaf and cuts out a small piece of the leaf for its case.
Distribution — Northeastern United States.
References — Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.
Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 75. 1914.

spurcella H. S., *Gelechia* ..... Fam. *Gelechiidae*
Hosts — *Prunus spinosa*, *Crataegus oxyacantha*.
Injury — Larva rolls leaves.
Distribution — Europe, Asia Minor.
Reference — Spuler, A. Schmetterlinge Europas, 2:361. 1910.

steinkelneriana Schiff., *Epigraphia* ..... Fam. *Gelechiidae*
Hosts — Crataegus, Sorbus, *Prunus spinosa*, Fraxinus.
Injury — Larva ties leaves together and eats them.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, 2:332. 1910.

stimulea Clem., *Sibine* (Saddle-back caterpillar) ..... Fam. *Limacodidae*
Hosts — Species a general feeder on fruit and forest trees, including Crataegus.
Injury — Larva eats foliage.
Distribution — Eastern North America.
References — Beutenmüller, William. Ent. Amer. 4:75. 1888.
Dyar, H. G., and Morton, E. L. New York Ent. Soc. Journ. 4:1. 1896.

strigata Müll., *Hemithea* ..... Fam. *Geometridae*
Synonym — *Nemoria aestivaria* Hüb.
Hosts — Quercus, Crataegus, Corylus, Syringa, Malus, Prunus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia, Japan.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 163. 1872.
Spuler, A. Schmetterlinge Europas, 2:5. 1910.

strigosa Fabr., *Acronycta* ..... Fam. *Noctuidae*
Hosts — Prunus, Crataegus, Rhamnus.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
Reference — Spuler, A. Schmetterlinge Europas, 1:137. 1908.

subsignarius Hüb., *Ennomos*.....Fam. *Geometridae*
(See page 1076.)

suffusana Z., *Notocelia*.....Fam. *Tortricidae*
Hosts — Crataegus, Prunus, Pyrus, Malus.
Injury — Larva ties together leaf cluster and feeds within, also eats leaf buds.
Distribution — Europe, Asia Minor.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, **2**:279. 1910.

superans Guen., *Acronycta*.....Fam. *Noctuidae*
(See page 1074.)

tesselaris A. and S., *Halisidota*.....Fam. *Arctiidae*
(See page 1073.)

textor Harris, *Hyphantria* (Fall webworm).....Fam. *Arctiidae*
(See page 1073.)

thysbe Fabr., *Hemaris*.....Fam. *Sphingidae*
Hosts — Viburnum, Symphoricarpus, Crataegus.
Injury — Larva eats foliage.
Distribution — Eastern North America.
References — Fernald, C. H. Sphingidae of New England, p. 16. 1886.
Beutenmueller, William. Hawk moths of the vicinity of New York City, p. 9. 1903.

tiliaria Harris, *Erranis* (Lime-tree spanworm).....Fam. *Geometridae*
(See page 1076.)

tineana Hüb., *Ancylis*.....Fam. *Tortricidae*
Hosts — Populus, Crataegus, Prunus, Malus.
Injury — Larva eats foliage after tying it with silk.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, **2**:270. 1910.

tirhaca Cr., *Pseudophia*.....Fam. *Noctuidae*
Synonym — *Ophiusa tirrhaea* Cr.
Hosts — Rhus, Pistacia, Crataegus.
Injury — Larva eats foliage.
Distribution — Southern Europe, Asia, Africa, Australia, and islands of southern Pacific.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, **1**:312. 1908.

titea Cram., *Phigalia*.....Fam. *Geometridae*
(See page 1076.)

trapezina Linn., *Calymnia*.....Fam. *Noctuidae*
Hosts — Quercus, Salix, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, **1**:244. 1908.

tridens Schiff., *Acronycta*.....Fam. *Noctuidae*
Hosts — Crataegus, Prunus, Malus, Rosa, Salix, Rhamnus, and other species.
Injury — Larva feeds on foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 208. 1872.
Spuler, A. Schmetterlinge Europas, **1**:137. 1908.

turnus Linn., *Papilio* (Tiger swallowtail) ..... Fam. *Papilionidae*
Hosts — Crataegus, Malus, Cydonia, Prunus, Betula, Tilia, Quercus, Salix, and other species.
Injury — Larva eats foliage.
Distribution — Eastern North America.
References — Saunders, William. Can. ent. **6**:2. 1874.
Packard, A. S. Fifth rept. U. S. Ent. Comm., p. 536. 1890.

unicornis A. and S., *Schizura* ..... Fam. *Notodontidae*
Hosts — Malus, Prunus, Crataegus, Ulmus, Populus, Corylus, Quercus, and other species.
Injury — Larva eats foliage.
Distribution — North America.
Reference — Packard, A. S. Nat. Acad. Sci. Memoir 1:203. 1895.

variegana Hüb., *Olethreutes* ..... Fam. *Tortricidae*
Hosts — Malus, Pyrus, Crataegus, Prunus, and other species.
Injury — Larva ties leaf clusters together and eats leaves and buds.
Distribution — Europe, Asia.
References — Newstead, R. Gard. chron. **1901**:342. 1901.
Theobald, F. V. Insect pests of fruits, p. 82. 1909.

vernata Peck, *Paleacrita* (Spring cankerworm) ..... Fam. *Geometridae*
Hosts — Ulmus, Malus, Crataegus, and other species.
Injury — Larva eats foliage.
Distribution — North America.
Reference — Wellhouse, W. H. Univ. Kans., Ent. Dept. Bul. 11:283. 1917.

vetusta Boisd., *Hemerocampa* (Western tussock moth) ..... Fam. *Lymantriidae*
Hosts — Malus, Prunus, Crataegus, Juglans, Quercus, and other species.
Injury — Larva eats leaves and sometimes young fruit.
Distribution — Pacific coast of the United States.
References — Branigan, E. J. State Comm. Hort. California. Mo. bul. 3:245. 1914.
Essig, E. O. Injurious and beneficial insects of California, p. 408. 1915.

viridana Walch., *Chariptera* ..... Fam. *Noctuidae*
Hosts — Prunus, Crataegus, Pyrus.
Injury — Larva eats foliage at night.
Distribution — Europe.
Reference — Spuler, A. Schmetterlinge Europas, **1**:204. 1908.

viridata Linn., *Nemoria* ..... Fam. *Geometridae*
Hosts — Calluna, Crataegus, Rubus, Quercus, Betula, Corylus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 235. 1872.
Spuler, A. Schmetterlinge Europas, **2**:4. 1910.

vulgata Haw., *Tephroclystia* ..... Fam. *Geometridae*
Hosts — Crataegus, Polygonum, Rubus, and other species.
Injury — Larva eats foliage.
Distribution — Europe, Asia.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 209. 1872.
Spuler, A. Schmetterlinge Europas, **2**:75. 1910.

vulgella Hüb., *Gelechia* ..... Fam. *Gelechiidae*
Hosts — Crataegus, Prunus.

Injury — Larva ties together a cluster of leaves and feeds within.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 210. 1872.
Spuler, A. Schmetterlinge Europas, **2**:358. 1910.

DIPTERA

absobrina Felt, *Rhizomyia*..... Fam. *Cecidomyiidae*
Hosts — Crataegus, Populus, *Prunus virginiana.*
Injury — Larva found in leaf gall.
Distribution — North America.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.

anthobia F. Loew, *Contarina*..... Fam. *Cecidomyiidae*
Host — *Crataegus oxyacantha.*
Injury — Solitary larva feeds in blossom bud, causing it to remain closed and swollen.
Distribution — Europe.
References — Ross, H. Die Pflanzengallen Mittel- und Nordeuropas, p. 132. 1911.
Bagnall, R. S., and Harrison, J. W. H. Ent. Soc. London. Trans. 1917:391. 1917.

bedeguar Walsh, *Cecidomyia* (Tufted thorn gall)..... Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larvae deform leaves with filamentous subglobular vein galls, 1 cm. long, generally found on the midveins.
Distribution — North America.
References — Walsh, B. D. Can. ent. **1**:79. 1869.
Felt, E. P. New York State Mus. Bul. 200:138. 1918.

cerasifolia Felt, *Mycodiplosis*..... Fam. *Cecidomyiidae*
Hosts — *Prunus virginiana*, Crataegus.
Injury — Larvae live in galls on hawthorn fruit caused by *Gymnosporangium clavipes*, and feed on the rust spores.
Distribution — North America.
References — Felt, E. P. New York State Mus. Bul. 200:152. 1918.
Wellhouse, W. H. Ent. news **30**:144. 1919.

circumdata Winn., *Perrisia*..... Fam. *Cecidomyiidae*
Host — *Crataegus oxyacantha.*
Injury — Larva lives in leaf gall.
Distribution — Germany.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 212. 1872.
Kieffer, J. J. Genera insectorum, fasc. 152, p. 75. 1913.

crataegi Winn,, *Perrisia*..... Fam. *Cecidomyiidae*
Host — *Crataegus oxyacantha.*
Injury — Colonies of larvae cause rosettes of deformed sessile leaves, which make trees and hedges unsightly.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 212. 1872.
Connold, E. T. British vegetable galls, p. 190. 1902.

crataegifolia Felt, *Hormomyia* (Thorn cockscomb gall)..... Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larva deforms leaf with a green or red gall 1 cm. long, shaped like a cockscomb.
Distribution — United States.
References — Felt, E. P. Journ. econ. ent. **1**:20. 1908.
Felt, E. P. New York State Mus. Bul. 200:136. 1918.
(Figs. 116 and 117, page 1032.)

crataegifolia Felt, *Lestodiplosis* (Hawthorn fringed-cup gall) . . . . Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larva causes a gall on leaf or twig.
Distribution — United States.
References — Felt, E. P. New York State Mus. Bul. 124:408. 1908.
Felt, E. P. New York State Mus. Bul. 200:138. 1918.
(Figs. 114 and 115, page 1081.)

excavata Felt, *Lasioptera* (Purple leaf blotch) . . . . . Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larvae deform leaves with green or reddish, blister-like mines, about 8 mm. in diameter.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.

hirta Felt, *Rhizomyia* . . . . . Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Species probably inquiline in blister mine made by *Lasioptera excavata*.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.

hudsonici Felt, *Winnertzia* . . . . . Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larva deforms leaf with stout, cup-shaped, fimbriate, unicellular gall.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.

pomonella Walsh, *Rhagoletis* (Apple maggot) . . . . . Fam. *Trypetidae*
Hosts — Crataegus, Malus, Vaccinium, Symphoricarpos.
Injury — Larva tunnels in fruit.
Distribution — Eastern North America.
References — Walsh, B. D. First annual report on noxious insects of Illinois, p. 30. 1868.
O'Kane, W. C. New Hampshire Agr. Exp. Sta. Bul. 171. 1914.
Severin, H. H. P. State Comm. Hort. California. Mo. bul. 7:430. 1918.

venae Felt, *Lobopteromyia* (Thorn vein gall) . . . . . Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larva causes oval, smooth, fleshy gall, 5 to 8 mm. long, on leaf vein.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.
(Figs. 118 and 119, page 1083.)

venitalis Felt, *Dicrodiplosis* . . . . . Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larva found in same gall with *Lobopteromyia venae*.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.

Cecidomyia sp. (a. 2727 Felt) . . . . . Fam. *Cecidomyiidae*
Host — Crataegus.
Injury — Larvae cause subglobose, greenish, sometimes confluent, frequently pointed, polythalamous vein galls, the under side reddish, diameter 3 mm.
Distribution — United States.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.

Cecidomyia sp. (a. 1840 Felt) (Thorn spindle gall) . . . . . Fam. *Cecidomyiidae*
Host — Crataegus.

Injury — Larva causes a spindle-shaped thickened gall on leaf vein, green or reddish, length 1 cm., diameter 2 mm.
Distribution — Eastern United States.
Reference — Felt, E. P. New York State Mus. Bul. 200:138. 1918.
(Figs. 120 and 121, page 1084.)

HYMENOPTERA

betuleti Klg., *Trichiosoma* ..... Fam. *Tenthredinidae*
Synonyms — *Cimbex crataegi* Wd., *Trichiosoma tibialis* Steph.
Host — Crataegus.
Injury — Larva eats foliage.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 211. 1872.
André, Ed. Species des Hyménoptères d'Europe, 1:27. 1879.

cerasi Linn., *Caliroa* (Pear and cherry slug) ..... Fam. *Tenthredinidae*
Hosts — Prunus, Crataegus, Pyrus, and other species.
Injury — Larvae skeletonize leaves.
Distribution — Europe, North America, Australia.
References — Slingerland, M. V., and Crosby, C. R. Manual of fruit insects, p. 214. 1914.
MacGillivray, A. D. Hymenoptera of Connecticut, p. 79. 1916.

collaris MacG., *Profenusa* (Cherry and hawthorn sawfly leaf miner) .... Fam. *Tenthredinidae*
Hosts — Crataegus, *Prunus cerasus*.
Injury — Larva mines in leaf, causing brown blister which may cover from a quarter to the whole of the upper surface of the leaf.
Distribution — Massachusetts, New York.
Reference — Parrott, P. J., and Fulton, B. B. New York (Geneva) Agr. Exp. Sta. Bul. 411. 1915.

druparum Boh., *Syntomaspis* (Apple seed chalcid) ..... Fam. *Chalcididae*
Hosts — Malus, Pyrus, Sorbus, Crataegus.
Injury — Oviposition punctures cause dimples in fruit, and larvae destroy seeds.
Distribution — Europe, North America.
References — Schlechtendall, D. von. Ztschr. Naturwiss. Halle **61**:415. 1888.
Cushman, R. A. Journ. agr. res. 7:487. 1916.
Woodruffe-Peacock, E. A. Naturalist (London), no. 753, p. 329. 1919.

flaviventris Retz., *Lyda* ..... Fam. *Tenthredinidae*
Synonym — *Lyda clypeata* Klg.
Hosts — Crataegus, Pyrus.
Injury — Larvae defoliate branches, feeding in colonies.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 206. 1872.
André, Ed. Species des Hyménoptères d'Europe, 1:516. 1879.

humeralis Fourc., *Cimbex* ..... Fam. *Tenthredinidae*
Synonym — *Cimbex axillaris* Pz.
Hosts — Crataegus, *Prunus padus*.
Injury — Larva feeds on foliage.
Distribution — Europe.
References — Kaltenbach, J. H. Pflanzenfeinde, p. 212. 1872.
André, Ed. Species des Hyménoptères d'Europe, 1:24. 1879.

padi Linn., *Priophorus* . . . . . Fam. *Tenthredinidae*
Hosts — Crataegus, Pyrus, Prunus, Malus, Sorbus, and other species.
Injury — Larva skeletonizes leaves.
Distribution — Europe.
References — André, Ed. Species des Hyménoptères d'Europe, 1:84. 1879.
Collinge, W. E. Manual of injurious insects, p. 219. 1912.

punctum-album Linn., *Macrophya* . . . . . Fam. *Tenthredinidae*
Hosts — Fraxinus, Ligustrum, Crataegus.
Injury — Larva feeds on foliage.
Distribution — Europe.
Reference — André, Ed. Species des Hyménoptères d'Europe, 1:359. 1879.

Four species of unidentified sawflies (pages 1086 and 1087.)

INDEX OF GENERA AND SPECIES

(Synonyms are in italics)

A

PAGE

Acalla contaminana ... 1113
holmiana ... 1116
Acrobasis nebulella ... 1117
Acronycta americana ... 10 3, 1109
dactylina ... 10.3, 1114
euphorbiae ... 1115
luteicoma ... 1073, 1119
occidentalis ... 1074, 1120
psi ... 1123
radcliffei ... 1074, 1124
strigosa ... 1126
superans ... 1074, 1127
tridens ... 1127
Aegeria pyri ... 1124
Agrilus politus ... 1106
sinuatus ... 1108
vittaticollis ... 1050, 1108
Agriotes pubescens ... 1066, 1107
Alsophila pometeria ... 1076, 1122
Alticopus galeazii ... 1107
Amphidasis betularia ... 1111
Amphipyra pyramidea ... 1123
pyramidoides ... 1074, 1123
Ancylis nubeculana ... 1077, 1120
selenana ... 1125
tineana ... 1127
Anisopteryx aescularia ... 1109
Anthaxia quercata ... 1107
Anthonomopsis mixtus ... 1105
Anthonomus decipiens ... 1103
flavicornis ... 1104
nebulosus ... 1068, 1105
pomorum ... 1106
profundus ... 1106
Aphis *avenae* (Amer. authors) ... 1098
avenae Fabr ... 1097
bakeri ... 1092
brevis ... 1092
crataegi Buck ... 1094
crataegi Kalt ... 1093
crataegi Koch ... 1093
crataegiella ... 1094
crataegifoliae ... 1064, 1094
crataegus-coccinea ... 1094
edentula ... 1095
fitchii ... 1098
mali ... 1098
malifoliae ... 1099
marutae ... 1096
oxyacanthae Koch ... 1097
oxyacanthae Schr ... 1098
padi ... 1097
pomi ... 1065, 1098
pyri ... 1093
ranunculi ... 1093
rumicis ... 1099
sorbi ... 1099
Apion pomonae ... 1106
Aporia crataegi ... 1113
Archips argyrospila ... 1077, 1110
Argyresthia ephippella ... 1115
nitidella ... 1120
oreasella ... 1078, 1121

PAGE

Argyresthia *pruniella* ... 1115
Argyroploce pruniana ... 1123
Aspidiotus hederae ... 1095
nerii ... 1095
ostreiformis ... 1097
oxyacanthae ... 1097
perniciosus ... 1065, 1098
piri ... 1098
Asteroscopus cassinia ... 1126
Automeris io ... 1073, 1117

B

Basilarchia arthemis ... 1110
astyanax ... 1110
Blastodacna curvilineella ... 1080, 1114
hellerella ... 1116
Brachionycha sphinx ... 1126
Brachys aerosus ... 1066, 1101
Bucculatrix crataegi ... 1113
pomifoliella ... 1079, 1122
Byturus tomentosus ... 1108

C

Cacoecia crataegana ... 1113
rosaceana ... 1078, 1125
rosana ... 1125
Caliroa cerasi ... 1086, 1131
Calligrapha multipunctata ... 1105
Calymnia trapezina ... 1127
Capsus medius ... 1097
Capua angustiorana ... 1109
Catocala blandula ... 1111
crataegi ... 1113
fulminea ... 1115
paranympha ... 1115
polygama ... 1122
Cecidomyia bedeguar ... 1129
sp. (a. 1840 Felt) ... 1082, 1130
sp. (a. 2727 Felt) ... 1130
Cemiostoma scitella ... 1125
Ceratocapsus pumilus ... 1099
Ceresa bubalis ... 1092
taurina ... 1063, 1100
Ceroplastes rusci ... 1099
Chalepus dorsalis ... 1103
Chariptera viridana ... 1128
Cheimatobia brumata ... 1111
Chermes quercus ... 1094
Chionaspis furfura ... 1065, 1095
Choragus scheppardi ... 1107
Chrysobothris femorata ... 1050, 1103
Cilex glaucatus ... 1116
Cimbex *axillaris* ... 1131
crataegi ... 1131
humeralis ... 1131
Cnephasia nubilana ... 1120
Coleophora anatipennella ... 1109
fletcherella ... 1079, 1115
hemerobiella ... 1116
malivorella ... 1079, 1119
tiliella ... 1109
Conotrachelus crataegi ... 1051, 1068, 1103

PAGE

Conotrachelus naso ... 1105
nenuphar ... 1105
posticatus ... 1106
Contarinia anthobia ... 1129
Coptodisca splendoriferella ... 1079, 1126
Corythucha *arcuata* ... 1095
bellula ... 1056, 1092
brunnea ... 1092
crataegi ... 1095
cydoniae ... 1095
Crambus oxyacanthae ... 1115
Crepidodera helxines ... 1067, 1104
Cryptocephalus bipunctatus ... 1050, 1101
Cydia pomonella ... 1122

D

Dasychira pudibunda ... 1123
Datana integerrima ... 1117
ministra ... 1075, 1119
Deraeocoris olivaceus ... 1097
Diaphnidia pellucida ... 1055, 1098
Diaspis piri ... 1092
Dibolia borealis ... 1067, 1102
Dichelia grotiana ... 1116
Dichelonycha elongata ... 1066, 1103
testacea ... 1067, 1108
Dicrodiplosis venitalis ... 1130
Diloba coeruleocephala ... 1112
Diphucephala colaspidoides ... 1102

E

Eccoptogaster pruni ... 1106
rugulosus ... 1107
Empoa querci ... 1062, 1099
rosae ... 1099
Empoasca mali ... 1061, 1096
Ennomos magnarius ... 1076, 1119
subsignarius ... 1076, 1127
Epetrimerus armatus ... 1090
Epiblema biscutana ... 1111
Epicnaptera americana ... 1075, 1109
Epidiaspis betulae ... 1092
leperi ... 1092
piricola ... 1092
Epigraphia steinkelneriana ... 1126
Epitrix cucumeris ... 1067, 1103
Erineum clandestinum ... 1090
oxyacanthae ... 1090
Eriogaster catax ... 1111
lanestris ... 1117
Eriophyes calycobius ... 1090
crataegi ... 1090
crataegi-vermiculus ... 1090
goniothorax ... 1053, 1090
pyracanthae ... 1090
pyri ... 1090
sp. No. 1 ... 1052, 1091
sp. No. 2 ... 1053
sp. No. 3 ... 1053
Eriosoma *crataegi* ... 1096
lanigera ... 1051, 1064, 1096
Erranis tiliaria ... 1076, 1127
Erythroneura obliqua ... 1061, 1097
Eulecanium pyri ... 1093
Eulia quadrifasciana ... 1078, 1124
Euproctis chrysorrhea ... 1112
Eupteryx vanduzei ... 1062, 1100
Euscelis curtisii ... 1061, 1094
Eutettix seminudus ... 1062, 1099
Euthrips tritici ... 1066, 1100
Exapate congelatella ... 1112

G

PAGE

Gastropacha quercifolia ... 1124
Gelechia spurcella ... 1126
vulgella ... 1128
Glossonotus crataegi ... 1063, 1093
Gonodontis bidentata ... 1111
Graphocephala coccinea ... 1061, 1093
Grapholitha janthinana ... 1117
kroesmanniana ... 1125

H

Halisidota caryae ... 1073, 1111
tesselaris ... 1073, 1127
Haltica carinata ... 1067, 1102
foliacea ... 1104
Hemaris thysbe ... 1127
Hemerocampa leucostigma ... 1075, 1118
vetusta ... 1128
Hemithea strigata ... 1126
Hercyna palliolalis ... 1114
Heterocampa manteo ... 1074, 1119
Heterocordylus malinus ... 1051, 1054, 1096
Hibernia aurantiaria ... 1110
bajaria ... 1110
defoliaria ... 1114
leucophaearia ... 1118
marginaria ... 1119
Holcophora fasciellus ... 1115
Horcias dislocatus ... 1054, 1095
Hormomyia crataegifolia ... 1082, 1129
Hyphantria textor ... 1073, 1127
Hyponomeuta padella ... 1121

I

Idiocerus crataegi ... 1094
fitchi ... 1061, 1095
lachrymalis ... 1061, 1095
maculipennis ... 1095
pallidus ... 1062, 1098
provancheri ... 1062, 1098
suturalis ... 1062, 1100
Idiostethus tubulatus ... 1108

L

Lamenia vulgaris ... 1063, 1100
Lasiocampa quercus ... 1124
Lasioptera excavata ... 1130
Laspeyresia prunivora ... 1051, 1078, 1123
Lecanium bituberculatum ... 1092
caprear ... 1093
corni ... 1065, 1093
coryli ... 1093
nigrofasciatum ... 1097
pruinosum ... 1098
Lepidosaphes ulmi ... 1065, 1100
Lestes viridis ... 1048, 1091
Lestodiplosis crataegifolia ... 1080, 1130
Limnobaris calva ... 1102
Limonius dubitans ... 1066, 1103
Liparis auriflua ... 1125
Lithocolletis betulae ... 1110
cerisolella ... 1112
concomitella ... 1112
corylifoliella ... 1113
crataegella ... 1113
malimalifoliella ... 1119
oxyacanthae ... 1121
pomifoliella ... 1112
prunivorella ... 1116
Lobopteromyia venae ... 1082, 1130
Lophopteryx cucullia ... 1114
Lycia cognataria ... 1076, 1112

PAGE

Lyda *clypeata* ... 1131
flaviventris ... 1131
Lygidea mendax ... 1051, 1055, 1096
Lygus communis ... 1054, 1093
ostryae ... 1055, 1097
pratensis ... 1055, 1098
univittatus ... 1055, 1100
Lymantria dispar ... 1114
Lyonetia clerkella ... 1112

M

Macrodactylus subspinosus ... 1108
Macrophya punctum-album ... 1132
Macrosiphum crataegarium ... 1093
crataegi ... 1063, 1094
Magdalis aenescens ... 1101
barbicornis ... 1101
cerasi ... 1102
nitidipennis ... 1105
pruni ... 1106
Malacosoma americana ... 1075, 1109
disstria ... 1114
neustria ... 1120
Melanoplus atlanis ... 1054, 1091
bivittatus ... 1054, 1091
femur-rubrum ... 1054, 1091
Melanotus sp ... 1066, 1108
Melinna pumila ... 1099
Mesoleuca lacustrata ... 1117
Mineola indigenella ... 1077, 1117
Miselia oxyacanthae ... 1121
Mycodiplosis cerasifolia ... 1129
Mytilaspis pomorum ... 1100
Myzus oxyacanthae ... 1097

N

Nacophora quernaria ... 1124
Nematocampa *filamentaria* ... 1118
limbata ... 1118
Nemoria *aestivaria* ... 1126
porrinata ... 1122
viridata ... 1128
Nepticula aterrima ... 1110
atricollis ... 1110
crataegifoliella ... 1114
gratiosella ... 1116
ignobilella ... 1117
nitidella ... 1120
oxyacanthella ... 1121
prunetorum ... 1123
pygmaeella ... 1123
regiella ... 1124
scintillans ... 1125
Nola cucullatella ... 1114
Notocelia suffusana ... 1127
Notodonta cucullina ... 1114
Notolophus antiqua ... 1110

O

Oecanthus niveus ... 1048, 1091
Olethreutes achatana ... 1109
chionosema ... 1077, 1112
variegana ... 1128
Ophiderma flavicephala ... 1063, 1095
Ophiusa tirrhaea ... 1127
Opisthograptis luteolata ... 1119
Orchestes rufus ... 1107
Ornix anglicella ... 1109
crataegifoliella ... 1114
geminatella ... 1116

PAGE

Ornix inusitatumella ... 1117
Orthotylus ornatus ... 1055, 1097
Otiorrhynchus caudatus ... 1102
crataegi ... 1103
Ovatus mespili ... 1096

P

Paleacrita vernata ... 1076, 1128
Pamene rhediella ... 1124
spiniana ... 1126
Pandemis heparana ... 1116
ribeana ... 1125
Paonias myops ... 1119
Papilio podalirius ... 1122
turnus ... 1072, 1128
Parlatoria oleae ... 1097
Pemphigus corrugatans ... 1063, 1093
Penthina robrana ... 1113
Perrisia circumdata ... 1129
crataegi ... 1129
Phenacoccus aceris ... 1091
betheli ... 1095
dearnessi ... 1095
Phigalia pedaria ... 1121
titea ... 1076, 1127
Philaenus lineatus ... 1061, 1096
Phycita nebulo ... 1117
Phyllobius maculicornis ... 1104
oblongus ... 1105
Physatocheila dumetorum ... 1095
Pineapple gall (maker unknown) ... 1085
Platysamia cecropia ... 1111
Poecilocampa populi ... 1122
Polydrusus impressifrons ... 1104
pterygomalis ... 1107
sericeus ... 1107
Porthesia similis ... 1125
Priophorus padi ... 1132
Prociphilus crataegi ... 1094
pyri ... 1099
Prodenia praefica ... 1122
Profenusa collaris ... 1131
Psallus ambiguus ... 1091
Pseudanthonomus crataegi ... 1103
Pseudophia tirhaca ... 1127
Psylla costalis ... 1093
crataegi Schr ... 1094
crataegi Först ... 1096
crataegicola Flor ... 1098
crataegicola Först ... 1096
mali ... 1049, 1096
melanoneura ... 1096
peregrina ... 1098
saliceti ... 1099
Pulvinaria *betulae* ... 1100
innumerabilis ... 1100
oxyacanthae ... 1100
vitis ... 1065, 1100
Pyrausta purpuralis ... 1123

R

Ramphus flavicornis ... 1104
oxyacanthae ... 1104
Recurvaria *crataegella* ... 1120
leucatella ... 1118
nanella ... 1051, 1120
Rhagoletis pomonella ... 1050, 1085, 1130
Rhizomyia absobrina ... 1080, 1129
hirta ... 1130
Rhodophaea advenella ... 1109
Rhopalosiphum pad ... 1097

PAGE

Rhopalosiphum prunifoliae 1065, 1098
Rhopobota naevana 1120
Rhynchites aeneovirens var. punctatus 1100
aequatus 1101
auratus 1101
bacchus Linn. 1101
bacchus Oliv. 1101
coeruleocephalus 1102
comatus 1105
conicus 1104
cyanicolor 1107
giganteus 1104
icosandriae 1104
olivaceus 1105
ophthalmicus 1108
pauxillus 1105
pubescens 1107
sericeus 1108
Rosalia alpina 1101
Rumia crataegata 1119

S

Saperda *bivittata* 1102
candida 1102
cretata 1103
favi 1103
Sawfly No. 1 ..... 1086, 1132
Sawfly No. 2 ..... 1086, 1132
Sawfly No. 3 ..... 1086, 1132
Sawfly No. 4 ..... 1087, 1132
Schizoneura americana 1096
Schizura concinna 1074, 1112
unicornis 1128
Scythropia crataegella 1113
Selenia lunaria 1118
Sesia *pyri* 1124
scitula 1076, 1125
Sibine stimulea 1126
Simaethis fabriciana 1115
pariana 1051, 1121
Sphecodina abbotti 1108
Steganoptycha signatana 1125
Strymon calanus 1111
liparops 1118
melinus 1119
Swammerdamia lutarea 1118
oxyacanthella 1118
Syneta albida 1101

PAGE

Syntomaspis druparum 1131
Systena marginalis 1067, 1105

T

Tachypterus quadrigibbus 1072, 1107
Taeniocampa gothica 1116
incerta 1117
instabilis 1117
Telea polyphemus 1122
Tephroclystia vulgata 1128
Tetraneura ulmi 1100
Tetranychus pilosus 1090
telarius 1051, 1091
Thamnotettix clitellarius 1061, 1092
Thecla falacer 1111
Thyridopteryx ephemeraeformis 1115
Tinea oxyacanthella 1115
Tischeria malifoliella 1119
Tmetocera ocellana 1078, 1120
Tortrix incisana 1117
laevigana 1125
Trichiosoma betuleti 1131
tibialis 1131
Trichiura crataegi 1114
Trichosea ludifica 1118
Trioza urticae 1100
Triphosa dubitata 1115
Trochilium myopiforme 1119
Typhlocyba crataegi 1094
Tymnes metasternalis 1105

V

Valeria oleagina 1121

W

Winnertzia hudsonici 1130

X

Xanthonia villosula 1067, 1108
Xylotrechus convergeus 1102

Y

Yponomeuta cognatellus 1112
padellus 1051, 1121

Z

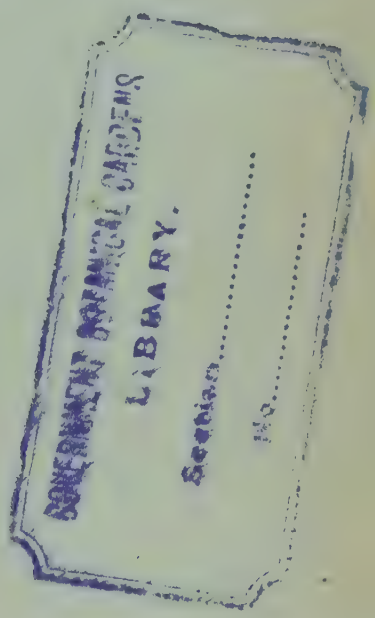
Zeuzera *aesculi* 1124
pyrina 1124

JUNE, 1922 MEMOIR 58

CORNELL UNIVERSITY
AGRICULTURAL EXPERIMENT STATION

THE BIOLOGY OF THE CHRYSOPIDAE

ROGER C. SMITH



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CONTENTS

PAGE

History of the family 1291
Method of study 1292
Life history of the Chrysopidae 1292
The egg 1293
The stalk of the egg 1294
Location 1295
Arrangement of the eggs 1295
Development of the embryo 1296
Hatching 1297
The egg burster in *Chrysopa oculata* 1298
The larva 1298
General characteristics 1298
Descent from the egg 1299
Molting 1300
First molt 1301
Later molts 1303
Morphology 1303
Habits 1306
Where found, and methods of concealment 1306
Trash-carrying larvae 1306
Foods 1310
Larval feeding 1311
Anal proleg of larva 1314
Larval excrement 1315
Classification of larvae 1315
The prepupa 1317
Location of the cocoon 1317
Spinning the cocoon 1317
The cocoon 1319
The pupa 1320
Color changes and later development 1321
Length of pupal life 1322
Emergence of the pupa 1322
The pupal molt 1323
The adult 1325
Expansion of the wings and darkening of the veins 1325
Voidance of larval excrement 1325
Tracheation 1325
Pupal tracheation 1325
Application of tracheation to wings of adults 1327
Foods 1328
Flight 1329
Activity of adults 1329
Cleaning the antennae and pulvilli 1329
Protective devices 1330
The sexes 1330
Sexual dimorphism 1331
Copulation 1331
Egg-laying after copulation 1332
Manner of oviposition 1333
Abnormalities in oviposition 1333
Length of oviposition period and number of eggs laid 1335
Length of life 1335

PAGE

Number of generations in a year 1335
Hibernation 1336
Discoloration in hibernating adults 1336
First appearance of the adults in the spring 1337
Factors reducing the number of individuals 1337
Parasites 1338
Egg parasites 1338
Larval parasites 1338
Pupal parasites 1338
Parasites of the adult 1341
Predacious enemies 1341
Factors affecting the spread of the species 1341
Economic importance of the family 1342
Description of the life stages of the species 1343
Chrysopa oculata Say 1343
Chrysopa nigricornis Burm. 1347
Chrysopa quadripunctata Burm. 1349
Chrysopa chi Fitch 1352
Chrysopa rufilabris Burm. 1356
Chrysopa plorabunda Fitch 1359
Chrysopa sp. 1361
Chrysopa lineaticornis Fitch 1361
Chrysopa bimaculata McClend. 1364
Chrysopa lateralis Guér. 1365
Chrysopa cockerelli Banks 1365
Other trash carriers 1367
Bibliography 1367

THE BIOLOGY OF THE CHRYSOPIDAE

THE BIOLOGY OF THE CHRYSOPIDAE[1]

ROGER C. SMITH

The insects included in the family Chrysopidae are of particular interest, first, because of their economic importance in destroying various small, soft-bodied noxious insects, spiders, and mites, and secondly, because of certain phases of their life history. Approximately sixty species of Chrysopidae have been designated in the United States. Several species in each locality can well be included in the list of common insects. They comprise one of the most homogenous families in habits and morphology to be found among insects.

The work herein described is based on the study of some fifteen species and covers a period of more than four years. The greater part of the work was done at Ithaca, New York, and additional collections and studies were made at Dayton, Ohio, at Milwaukee, Wisconsin, at Charlottesville, Virginia, and at Manhattan, Kansas. Through the courtesy of Dr. Nathan Banks, the writer was permitted to study the chrysopid types of Hagen, Fitch, and Banks now in the Museum of Comparative Zoology at Cambridge, Massachusetts.

Acknowledgment is made to Professor James G. Needham, of Cornell University, under whose direction this work was done. Further acknowledgment is made to Professor William A. Riley and to Mrs. R. C. Smith.

HISTORY OF THE FAMILY

Réaumur (1737) gave the first general discussion of this family, along with a discussion of the Hemerobiidae. This included a brief account of the habits, and a description, of three kinds of larvae. Linnaeus (1758) grouped the Chrysopidae with the Hemerobiidae under the name of the latter in his tenth edition of the *Systema Naturae*. The systematic position of the family remained unchanged until 1815, when Leach designated the family Chrysopidae, with the one genus Chrysopa, the name being derived according to Schneider (1851) from *Hemerobius chrysopis*.

Schneider's excellent monograph marked the real beginning of the modern classification of the family. From that time to the present, many species have been described by Brauer, Hagen, McLachlan, Petersen, and Navas.

In the United States, among the early writers was Fitch (1855), who gave a very excellent account of the Chrysopidae. He discussed the life history and biology of the species in New York State, and described all the species he could find. Hagen (1861) listed and described thirty-

[1]Also presented to the Faculty of the Graduate School of Cornell University, June, 1917, as a major thesis in partial fulfillment of the requirements for the degree of doctor of philosophy.

eight species, all under the genus Chrysopa except *Meleoma signoretti*. Banks (1903 and 1907) gives the present classification of the family, with the exception of some new species added since. He has contributed nearly all the descriptions of American species since Hagen's time.

METHOD OF STUDY

In these studies, chrysopid adults were confined in vials and lamp-chimney cages over growing plants, for oviposition. The vials (Plate LXXXV, 1) were plugged with cotton, and the chimneys were covered with several thicknesses of cheesecloth held in place by a rubber band. All adults and larvae were fed daily with the food on which they appeared to thrive best, which was in general the smaller aphids. The cabbage aphis, *Aphis brassicae*, was preferred for both larval and adult food. A constant supply of these insects was kept available on young cabbage plants throughout the fall, winter, and spring of each year. During the summer almost any species of aphid close at hand was used. A few drops of water in the vials was apparently relished by both larvae and adults. It was found advisable to occasionally moisten the cotton plugs of vials containing cocoons, in order to prevent the death of the pupae by desiccation.

All descriptions, photographs, and drawings of larvae were made by the writer from live material. Most of the photographed larvae were magnified from five to seven times and were but slightly reduced in reproduction. All drawings were outlined with a camera lucida. The drawings of corresponding parts were, with a few apparent exceptions, drawn to the same scale, so that they may be compared with one another as to size. Special effort was made to bring out identification characters in the illustrations. The dorsal setae have in most cases been extended forward. When studying a larva, the direction of these setae will be seen to vary with the position of the larva in the microscopic field. In reality, those over the thorax extend vertically, while those over the abdomen extend slightly caudad (Plate LXXV, 1).

LIFE HISTORY OF THE CHRYSOPIDAE

Most of the published information concerning the biology of this family is contained in brief notes by many writers. The two papers of Lurie (1897 and 1898) in Russian are important contributions. The most noteworthy work done in America is that of Fitch (1855), and that of Wildermuth (1916) on *Chrysopa californica*. The following references give either life histories or valuable biological information concerning the Chrysopidae, those marked with an asterisk being American papers.

Alderson, 1911—*Chrysopa dorsalis.*
Brauer, 1867—*C. pallida.*
*Fitch, 1855—*C. novaeboracensis* and others.
Froggatt, 1904—*C. ramburi.*
*Garman and Jewett, 1914—*C. oculata.*
*Howard, 1901—*C. oculata.*
LaCroix, 1921—*C. perla.*
*Lelong, 1890—*C. californica.*
Lurie, 1898—*C. septempunctata.*
*McGregor and McDonough, 1917—*C. rufilabris.*
*Marlatt, 1895—*C. oculata.*
Perkins, 1905—*C. microphya.*
Réaumur, 1737—General.
*Shimer, 1865—*C. illinoiensis.*
Van der Weele, 1909—*C. jacobsoni.*
*Weed, 1897—*C. oculata.*
*Wildermuth, 1916—*C. californica.*
Zehntner, 1900—*Chrysopa* sp.

The species studied biologically during their whole life history, or in part, for this account are as follows: *Chrysopa oculata* Say; *C. oculata* (Say) var. *albicornis* (Fitch); *C. oculata* (Say) var. *chlorophana* (Burm.); *C. chi* Fitch; *C. chi* (Fitch) var. *upsilon* (Fitch); *C. nigricornis* Burm.; *C. rufilabris* Burm.; *C. interrupta* Schn.; *C. quadripunctata* Burm.; *C. plorabunda* Fitch; *C. harrisii* Fitch; *C. lineaticornis* Fitch; *C. lateralis* Guér.; *C. bimaculata* McClend.; *C. cockerelli* Banks; *Meleoma signoretti* Fitch; *Allochrysa virginica* Fitch. The keys given by Banks (1903) will be found adequate for separating these genera and species.

Two species, *Chrysopa oculata* with its varieties, and *C. nigricornis,* have served almost equally as a basis for this account. These two were chosen because they are of wide distribution and because they represent two different habitats, the former being a garden and field species and the latter a tree species.

THE EGG

The eggs of the chrysopid species seen can be readily recognized and distinguished from the eggs of other insects by the fact that they are attached normally to a hyaline, hardened gelatinous stalk from four to eight millimeters long. The egg proper is elongate-elliptical in shape and green to yellowish green in color.

There is a difference in the size of the eggs of different species, as well as in the length of the stalk. There appears to be a slight variation also

in the color at deposition in some of the species, but the arrangement and the situation in which they are found have thus far been most useful in identification.

The color of the egg very closely simulates the green color of leaves. At first the eggs are of the same shade as is shown by the under side of most leaves of plants. As the embryo develops, the egg becomes gray with darker areas, but this change of color does not make it any more conspicuous.

The anterior pole of the egg is somewhat flattened. In the middle of this flattened area is the prominent, raised, button-like micropyle. The micropyle is circular and its center is depressed. The broad border is divided into from thirty to forty minute triangular ridges, with their outer borders rounded. The micropyle in *Chrysopa nigricornis* and that in *C. oculata* show exactly the same characteristics. It is white at all stages, but in freshly laid eggs it may have a slight greenish tinge.

The stalk of the egg

The egg stalk is composed of a hyaline gelatinous substance, which hardens somewhat after exposure to the air for a few seconds. In midsummer the stalks fail to harden to the same degree, due probably to the higher temperature. Then the stalk material may be drawn out like glue into a fine, clear thread. At all seasons the stalk hardens sufficiently to furnish a fairly rigid support for the egg and to withstand a strong wind. It is usually attached at the extreme posterior end of the egg, but in exceptional cases it may be attached to the side of the egg.

Usually there is one egg to a stalk, but confined females occasionally deposit an egg attached to the stalk or on the egg proper of a previously deposited normal egg. In one instance noted, two stalks were attached to the stalk of a previously deposited egg; in another instance, an unstalked egg was found adhering to a stalked egg.

The length of the stalk appears normally to vary directly as the length of the abdomen of the female. *Chrysopa nigricornis* was the largest species studied, and *C. plorabunda* the smallest. The stalks of the eggs of the former were the longest (from 7.57 to 8.6 millimeters), and those of the latter were the shortest (from 2.46 to 3.82 millimeters). Females in confinement, however, often deposit eggs on stalks half, or less than half, the normal length. Stalkless eggs are not uncommon, but these are evident abnormalities.

It is usually stated that the stalk is a protection against parasites and predatory enemies, particularly the larvae of their own kind. Eggs lying on a leaf are attacked as soon as the larvae become active, while the stalked eggs are generally the last discovered. Leaf crawlers, such

as Coccinellidae, Chrysomelidae, and various lepidopterous and hymenopterous larvae, are less likely to crush or to eat stalked eggs than unstalked ones. On the other hand, newly hatched and later first-instar larvae can ascend an egg stalk and exhaust the contents of the egg or the embryo. Generally speaking, newly hatched larvae first seek aphids or other food on the leaf surface, and climb the stalks after failing to find food there. Ants can climb up the stalks or bend them over and devour the eggs. They were very troublesome in outdoor rearing cages. Several species of hymenopterous parasites have been bred from chrysopid eggs. It is thus seen that the stalk offers only partial protection.

Location

Eggs may be deposited in a great variety of situations, depending on the species. The usual place is on plants provided with food for the larvae, not because the adult has the intuition to deposit them there, but because she goes to these plants to feed, and, being there, she deposits her eggs. Some of the less common species did not oviposit in confinement, but most species oviposited freely.

Some eggs have been observed in very unusual places. The shades and supports of the electric lights visited during the summer were often observed to have eggs deposited on them. Hundreds were deposited constantly in these unfavorable places. These eggs developed just as did eggs more favorably located, the empty shells always being found. A student reported that a female Chrysopa flew in through his open bedroom window when the light was on in the evening, and the next morning he found eggs deposited on his coat, which was hanging over a chair. In another student's room, the writer observed two hatched Chrysopa eggs on the chandelier. Brick and stone walls near lights and near aphid-infested plants were frequently found to be places of oviposition. Since the larvae are very active, some of those hatching in such unfavorable places undoubtedly succeed in finding food, but many must perish.

Arrangement of the eggs

Eggs laid in the open generally do not have a definite arrangement. Occasionally a straight row of ten or fifteen almost equally distant may be found across a leaf or on a plant stem. Otherwise the eggs are deposited singly or in irregular groups at varying distances apart. *Chrysopa nigricornis* generally deposits its eggs in rather closely arranged, irregular groups on leaves of maples, spiraea, and other plants. Not infrequently they are in irregular tangled masses without any definte arrangement. Such groups can often be identified posi-

tively in the field as eggs of this species, but single eggs are not unusual.

Most of the eggs of *C. quadripunctata, C. rufilabris, C. chi,* and others of the more uncommon species, are laid singly. *C. oculata* and its varieties lay their eggs either singly or in irregular groups.

Eggs from fertilized females in rearings nearly always hatch, the hatching percentage approaching 100 if conditions are not decidedly unfavorable. In early spring and late fall rearings, the hatching percentage is lower. In one case in which 95 eggs were laid in the laboratory in February, 1916, by *C. oculata,* only 37 or 39 per cent hatched. This is an extremely low percentage, and was undoubtedly due to unfavorable temperature during the cold nights of February and March. However, examination of the unhatched eggs showed that the embryos of some were partly developed. No eggs from unfertilized females have hatched. They shrivel early, but retain their bluish green color.

In two experiments, eggs of *C. oculata* that were completely submerged up to nineteen hours, hatched, but eggs submerged in water for from twenty-four to forty-eight hours all failed to hatch. It is very probable that eggs can withstand considerable rainy weather and submergence for a short time as a result of floods, without injury.

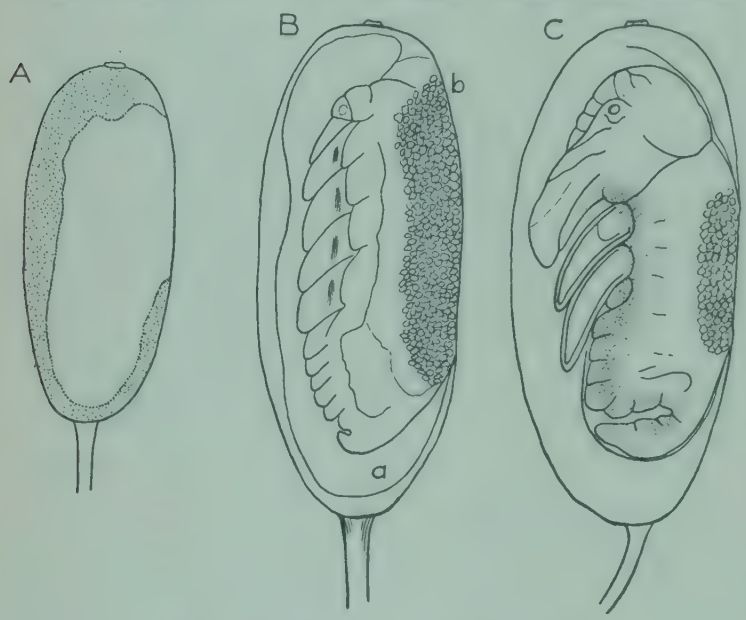


FIG. 154. EGGS AT VARIOUS STAGES

A, Lateral view of egg of Chrysopa oculata after thirty hours development, showing how the abdomen extends around on the dorsum in the early stages of development. B, Lateral view of egg of C. nigricornis after about ninety hours development, showing shortening of abdomen (a) at turning. C, Egg of C. nigricornis showing abdomen pushing forward toward the venter, thus completing the turning

Development of the embryo

The development of the embryo can be observed readily in Chrysopa eggs. The embryology has been the subject of short articles by several writers, among them Packard (1871 and

1872) and Tichomirowa (1890). The embryological observations made in the course of the present studies are not included in this account.

The chief point observed in the embryology which has not been described, it is believed, is the turning or partial turning of the embryo. The germ band develops on the venter of the egg, with the area destined to be the end of the abdomen extending around the posterior pole of the egg and part way up the side of the dorsum. At thirty hours the abdomen can be seen clearly in this position on the basal dorsal part of the egg. As development proceeds, the abdomen shortens and is drawn up in a fold at the posterior pole. As the dorsum of the embryo continues to envelop the yolk mass, the contracted abdomen pushes forward and comes to lie on the venter of the egg, reaching nearly to the tips of the jaws. The dorsum of the embryo has by that time enveloped the yolk mass and lies next to the chorion. This is the position of the embryo at hatching.

The large black ocellar areas appear very prominent in eggs ready to hatch, at the anterior end of the egg on each side of the midventral line. There is a lateral indenture of the chorion on each side extending nearly the length of the egg. There is a series of three or more somewhat triangular, very dark to black, bars at the sides. The egg burster can be seen as a narrow black line between the eyes in the midventral line.

There is considerable variation in the length of the period of development within the species. Temperature is undoubtedly the most important factor, as this variation is between different batches of eggs and is only slight in the same group. Eggs laid in the late fall or early spring were found to be the longest in development. The longest and the shortest records of embryonic development for a few species studied were: for *Chrysopa oculata,* from 5 to 12 days; for *C. nigricornis,* from 4 to 7 days; for *C. quadripunctata,* from 4 to 6 days.

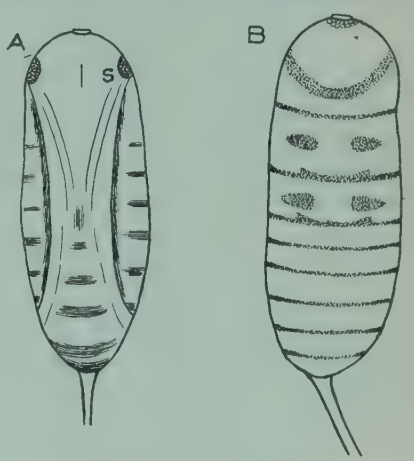


FIG. 155. EGGS OF CHRYSOPA OCULATA

A, Ventral view of egg ten minutes before hatching, showing the egg burster (s) in position. B, Dorsum of an egg ready to hatch

Hatching

One can readily ascertain when an egg will hatch by the distinctness with which the egg burster appears. Just before hatching, it is dark or black and one can scarcely tell whether it is through the chorion or just beneath it.

The embryo pushes the burster through the chorion to its entire length, and may by upward shifts widen the rent. Then its head is forced through the rent, causing the chorion to tear above. The head of the embryo bursts through the embryonic molt at this time or earlier, so that the molt, with the burster, is left behind. The molt is attached to the inside of the chorion in the midventral line. The mouth parts and the legs retard emergence so that the larva forms a loop over the egg. The mouth parts are slowly withdrawn from the molt, and then the larva emerges fully with the exception of the end of the abdomen. The larva then rests supported by the tip of the abdomen until the chitin hardens, and in a half hour from the beginning of hatching it is ready to descend from the shell. (Smith, 1922.)

The egg burster in Chrysopa oculata

The egg burster may be readily studied by picking out the embryonic molt from the lower part of the opening in the egg shell and mounting it in glycerin jelly or balsam. The burster is a thickening and specialization of the chitinous embryonic molt over the anterior mid-dorsal region of the head of the embryo. The burster proper is almost transparent and is 0.118 millimeter long and 0.029 millimeter wide at the lobe. In cross section it would appear V-shaped with the apex outward. Along the front border is a row of very small teeth which suggest a saw. The number of teeth varies from twenty to thirty and they are irregularly spaced. On the upper part is a prominent projection, referred to as a *lobe*. This lobe may or may not have a short, sharp tooth at its apex, but it bears teeth on the under side. The bursters of the species studied are all of this type.

FIG. 156 EGG BURSTER OF CHRYSOPA NIGRICORNIS. LATERAL VIEW

THE LARVA

General characteristics

The larva at hatching is about 2 millimeters long, is sparsely beset with long setae, and is predominately gray in color. The average measurements of five newly hatched larvae of *Chrysopa oculata* were as follows:

Total length of larva	1.88 millimeters
Length of head	0.54 millimeter
Length of mandibles	0.34 millimeter
Width of head	0.33 millimeter
Width of body at metathorax	0.38 millimeter
Length of longest setae on body	0.47 millimeter

One can distinguish the first instar of all species in an easier and quicker way than by measurement. The lateral tubercules on prothorax and abdomen bear two setae each in this instar. The meso- and metathoracic tubercles bear three large setae each. But in no case are there from five to fifteen, as in the other instars. *C. oculata* and its varieties, and *C. chi* and its variety, have on the dorsum of the head a large black spot covering most of this area and broadening out to the bases of the antennae. This spot persists in the second instar, but in the third it breaks up into three spots. A few specimens show even in the first instar the future lines of separation, so that they may at times appear slightly disconnected. This large spot on the head, therefore, taken in connection with the size, will often indicate the instar at a glance. The head spots of the first-instar larvae of the other species studied are the same as in the second and third instars, and therefore the lateral setae furnish the more reliable index.

The color of the body changes gradually, so that at the end of the first instar the larva has, more or less distinctly, second-instar coloration. Larvae that have when mature a dark metathoracic region, begin to show this coloration about midway in the first instar. Abdominal coloration appears also at this time. But in all larvae the anterior part of the abdomen, regardless of future colors, appears smoky to black. This darkening is due to the food in the mid-intestine and appears with the first meal. In newly hatched larvae the green yolk can be seen in the mid-intestine at the posterior part of the thorax and the anterior part of the abdomen.

The legs, the jaws, and the antennae are nearly hyaline at hatching. Very soon the tips of the jaws become amber-colored, indicating chitinization. The legs and the antennae also darken slightly.

The lateral and dorsal setae serve both as a protection and as sense organs. When one of these setae is touched, the larva bends away from the object. If touched again the larva moves still farther away, or becomes frightened and runs away. The body of the larva can scarcely be touched without the larva's being apprised of the approach through these radiating setae. The dorsal setae serve to protect the dorsum, while the lateral ones protect the sides. The strong jaws are in front, and the abdomen can be retracted in part, so that the larva has a fair degree of security from its enemies.

Descent from the egg

The larva, after resting on the egg shell for from fifteen minutes to several hours, begins to walk around over the shell, at times reaching upward and outward in an effort to locate something near at hand by

which it can leave the egg. It holds fast by the tail except when bringing the abdomen forward; then it braces itself securely with its legs. It becomes more and more restless on the egg. Finally, after walking around over the egg, it discovers the egg stalk. If the stalk be perpendicular, the larva generally goes down head first, holding fast by the tail and grasping the stalk by the claws. Sometimes definite steps are indicated by the tail, but oftener this fails to hold and then it catches itself. The larva may come down backward, but this method appears to be less frequent. If the stalk be leaning or horizontal, the larva swings around on it and walks to the supporting surface upside down and head first. It grasps the stalk as a sloth grasps the limb of a tree. It does not use the tail in this case. Some writers suggest that the larva may drop from the egg. Lurie (1898), however, has stated correctly that dropping from the egg is not the normal manner of descent.

The larva is usually hungry by the time it comes down from the egg, and immediately it begins to search for food. If none is provided, it starves to death in about a day, or at most two days, after hatching. Small aphids, such as cabbage aphids, are best suited for feeding newly hatched larvae. Insects' eggs, such as those of aphids and of the corn-ear worm moth, have also been used in rearings.

If a leaf having on it a group of eggs ready to hatch is left in a vial, the cannibalistic habits of the larvae will be demonstrated. In the same batch of eggs, those first deposited or those developing most rapidly will hatch first. If the larvae are undisturbed and are not fed, they will attack the unhatched eggs and then one another. In one instance forty-one eggs were allowed to hatch. After a few days there was but one live larva, the others having been killed by it or by its companions.

Molting

All chrysopid larvae have been observed to molt three times, the last molt occurring within the cocoon. This does not include the embryonic molt, which occurs at hatching.

The first molt takes place from two to seven days after hatching. The second molt usually occurs at a somewhat shorter interval, from two to five days. The third instar may be very prolonged. Spinning usually takes place from four to ten days after the second molt. The final larval molt within the case occurs from five to fifteen days after spinning, or, in the case of wintering forms, from four to eight months after spinning.

First molt

In *Chrysopa oculata*, the appearance of the chitin at the time of the molting is shining and glassy. On closer study, the stout setae so characteristic of second-instar larvae can be seen regularly folded across the body beneath the old first-instar cuticula. The setae of the prothoracic tubercles are folded ventrad and caudad. They fold, therefore, around the body, and come together on the midventral line. Where it occurs, this prominent black line on the venter is one of the best indices of early molting. The setae of the other thoracic and the abdominal tubercles are folded across the dorsum. They are dark to black, and become fairly distinct just before molting. The old setae appear wholly black and somewhat shriveled. The ends of many are bent downward or broken. Most of them appear to be more or less withered. The coloration of the second instar can also be seen, but instead of appearing sharp and brilliant, the colors are dull and indistinct.

Just prior to molting, the larva takes no food. Some time before molting, it generally engorges with food; but just prior to the process, aphids may walk over the larva without being attacked. The larva also experiences some difficulty in walking at this time. It appears that the pulvilli do not adhere well to the substratum; their hold slips, and apparently the anal secretion is too copious and this also retards them. In all species the head capsule is somewhat distorted, especially posteriorly.

As a typical case the molting of a first-instar larva of *C. oculata*, as observed under the highest-power binocular, is here described. This larva was observed to be ready to molt, and with a camel's-hair brush it was removed to a slide. Soon there was noted a drop of a gelatinous anal secretion, which held the tail to the slide. The larva began to twist and pull. The legs appeared to be practically useless. The segments of the tail began to contract as units, in regular order, beginning with the last and going forward about every seven seconds. This continued for four and one-half minutes. The end of the abdomen was then seen to free itself of the molt, which was shown by a shift forward. The contractions continued, and in a half minute the cuticula was free over the thorax and the abdomen also. It must next be forced open. The body was pulled forward by a series of wavelike contractions, comparable to those seen in the hatching embryo and the molting pupa. With each forward pull there was left a little more clear space in the tail region, and the thorax became more distended. The old cuticula during this process remained securely cemented to the slide by the end of the abdomen, this constituting the fixed point on which the larva pulled. After three or four rapidly repeated shifts, a split began on the mid-dorsal

line at the posterior part of the prothorax. This occurred six minutes after the abdomen was cemented to the slide. The split lengthened rapidly, both anteriorly and posteriorly. At the same time the thorax began to arch, the head was bent ventrad, and the abdomen was pulled forward. In two minutes more the mouth parts were very carefully and slowly withdrawn. The head was lifted slowly with the arching of the thorax, and during this process the legs were being withdrawn also. The tracheal chitinous intima was drawn out through the spiracles as hollow threads. The jaws and the antennae freed, the legs were pulled entirely out, the metathoracic legs being the last to appear. By this time the abdomen was practically out of the skin. The whole process to this stage required eight and a half minutes. As the old skin moved backward, the setae, folded across or around the body, thus freed, sprang into their normal positions.

The newly molted larva is very helpless, similar to its condition at hatching. The legs cannot be used. The head is bent ventrad and caudad. The larva holds fast to the molted skin by means of the anal proleg, which constitutes its only support while the new chitin is hardening. The legs are pulled up and then extended occasionally, and the head is slowly lifted to a horizontal position. The larva under observation rested on its legs and the head was in the normal position in twelve minutes from the beginning of the molt.

The old larval skin remained attached to the slide, the end of the tail being flattened and glued fast. There was a rent in the cast skin from the mesothorax to the head; in fact, only the venter of the thorax remained intact. The legs were pulled up and were wholly under the venter, except the last pair, which protruded slightly. The black patch on the head was retained. It is generally possible to name the species of the larva and the instar from the old larval skin. However, the color pattern is not well retained. In rearings, the molted skins were usually found in the vials adhering to the glass or to the cotton plugs.

The coloration of the body is that which is characteristic of the instar. The color pattern is distinct, of the greatest intensity during the instar. The grays at this time appear white to semi-translucent and often yellowish. The color pattern on the head is represented at molting, as at hatching, by an indistinct brownish patch. After an hour the outline of the black patch is distinct, but from two to four hours must pass before the normal head and body coloration is complete. The mouth parts, palpi, antennae, and legs are from wholly hyaline to translucent. The tips of the jaws become yellowish brown in an hour. The darkening of the leg segments appears slowly also.

Food offered to the larva up to forty-five minutes after emergence was rejected, but at the end of one and one-half hours the larva attacked a large aphid of its own accord and exhausted the fluids.

Later molts

About four days after the first molt, another molt occurs. The second molt is effected exactly like the first.

The final molt cannot be observed through the cocoon, but one can readily tell when the larva has pupated by the dark disk at the bottom of the cocoon. If a cocoon showing this disk be opened, it will be seen that the disk is the last larval skin which is pushed off the abdomen and rests at the bottom of the case. This molt may be observed if the larva fails to spin a cocoon, which can be brought about by disturbing it while it is spinning. It generally refuses to spin further if disturbed, and coils up in the bottom of the vial and pupates (Plate LXXXVII, 16). The old larval skin splits over the thorax, and by the raising and lowering of the head the skin is slowly moved back (Plate LXXXVII, 5). Further movements up and down on the thorax and the abdomen cause the skin to slip over the abdomen, and it finally rests near the end of the abdomen at the bottom of the cocoon.

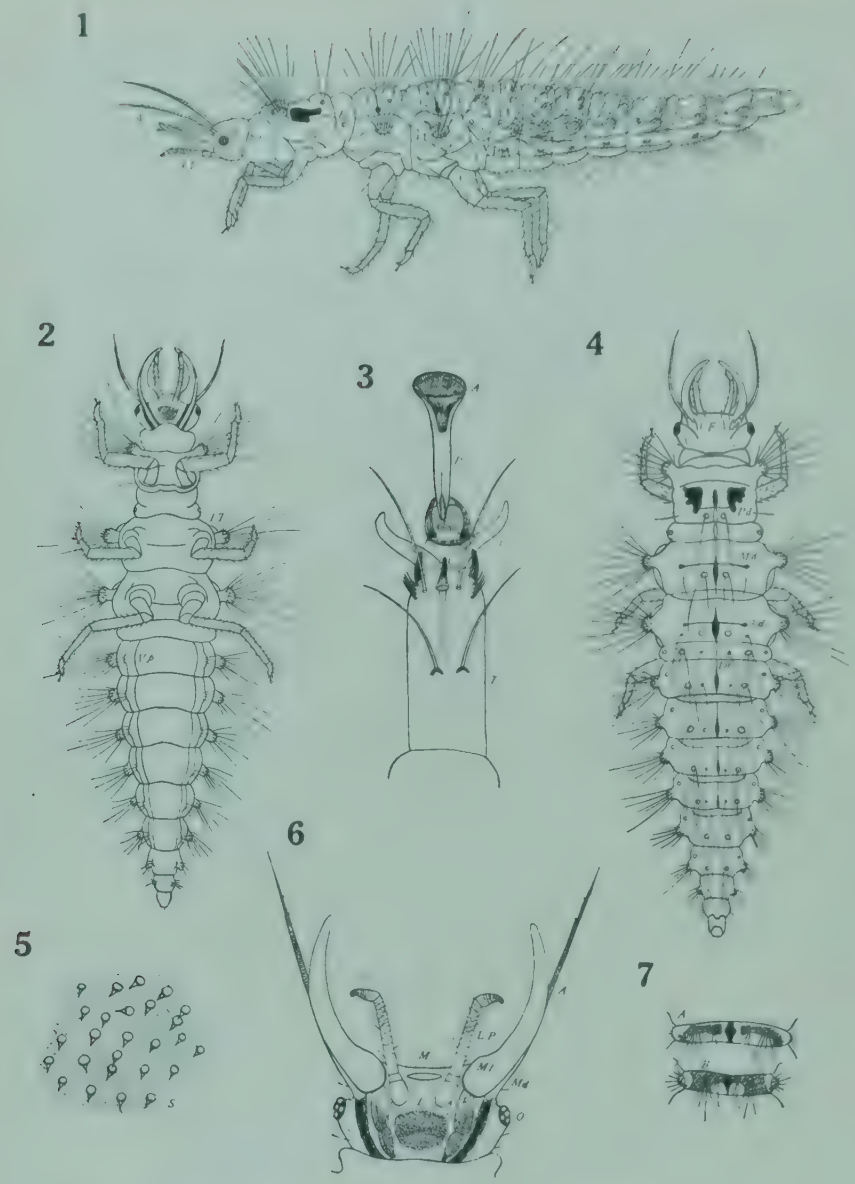
The trash carriers present complications in the molting process in that they carry packets of debris on their backs. In the few cases observed, the packet was cast off at the molting time and was reformed of fresh materials. If there were no fresh materials provided, the old packet was reappropriated. Lefroy (Lefroy and Howlett, 1909) described a similar form in India which carried such a packet, and stated that the packet was shed with each molt and was reformed from new materials.

Morphology

A number of very interesting features are illustrated by the morphology of the larva. The original somewhat detailed account must be omitted for the sake of brevity, and only a few features are here included.

Perhaps the most striking specialization in the family is the prolongation of the maxillae and the mandibles to form sucking tubes. These are held together by a flange which fits into a groove, and the small canal between them serves to convey their liquid food to the pharynx. The true mouth is mechanically closed, but may be opened by probing with a dissecting needle. It is somewhat reduced in size.

In the thorax and the abdomen, each segment is made up of two parts, or subsegments, which are in most cases quite apparent. The anterior subsegment is very much smaller than the posterior one. The



CHRYSOPA OCULATA AND C. NIGRICORNIS

1, Side view of a third-instar larva of Chrysopa oculata (A, antennae; J, jaws; Lp, labial palpi; O, ocellar field; S1, first subsegment, S2, second subsegment, of prothorax; lt, lateral tubercle; Ps, mesothoracic spiracle; dp, dorsal papilla; dt, dorsal tubercle; vp, ventral papilla)

2, Ventral view of same larva (LT, lateral tubercle; Vp, ventral papilla)

3, Tarsus and pulvillus of third-instar larva of C. oculata (A, arolium; P, plantula; C, claw; T, tarsus)

4, Dorsal view of larva shown in 1 and 2 (Pd, prothoracic depression, Md, mesothoracic depression, 3d, metathoracic depression, all probably apodeme invaginations; Db, dorsal blood vessel; A, antennal sclerite; F, front; S, spiracle)

5, External appearance of cuticula of a mature larva, under high magnification (S, spinules)

6, Ventral view of head of third-instar larva of C. oculata (A, antenna; Md, mandible; Ml, maxilla; LP, labial palpus; M, mouth opened by dissection; L, labium; O, ocellar field; 1, probably stipes of maxilla; 2, probably cardo of maxilla)

7, First abdominal segment (A) of C. oculata, showing no lateral tubercles, and (B) of C. nigricornis, showing very small lateral tubercles

first abdominal segment has been generally mistaken for a subsegment of the metathorax. There are without doubt ten abdominal segments in all the larvae. The last two segments are somewhat tubular and are retractile, or telescopic.

The dorsal blood vessel is very distinct in all species seen. It extends along the mid-dorsal line from the prothorax to the seventh or the eighth abdominal segment. The vessel is usually black to grayish, or even amber-colored. Pulsations can be readily seen in the middle part.

The pulvillus presents another modification. This is a trumpet-like structure, resembling the so-called "sucker" seen in many of the sarcoptic mites. The larva uses these pulvilli in walking on glass or other smooth surfaces, in which case the pulvilli are bent or twisted as if they were of rubber. It is usually stated that they adhere by suction, but the absence of strong musculature and the irregular border of the arolium appear to be against this view. Furthermore, no trace of any secretion could be seen by repeated observations with magnifications of all powers including an oil-immersion lens. Dewitz (1884 b) held the view that there was a secretion.

The species differ but little in morphology of the larva. The first segment of the abdomen in *Chrysopa nigricornis* has definite small lateral tubercles, while in other species thus far seen the lateral tubercles are very much smaller or are lacking in this first abdominal segment. The other lateral tubercles differ in size in the various species. In *C. rufilabris* they are very small, in *C. plorabunda* they are of medium size, in *C. oculata* they are large. The stalks are short in *C. rufilabris*, medium in the *oculata* group, and very long and slender in the trash carriers *(C. lineaticornis* and others). The trash carriers have also a much shorter and somewhat humped abdomen in comparison with the *oculata* type. The modification of the abdominal setae and tubercles fits the larva admirably for carrying its packet. In *C. cockerelli* there are from one to three rows of microscopic hooked setae on each abdominal segment to the seventh, which assist in holding the packet in position.

There is a difference in the color of the setae from the lateral tubercles. They are all colorless in *C. plorabunda* and *C. quadripunctata*; in *C. nigricornis* all are colorless except the two large central ones, which are black; in *C. oculata* and *C. chi,* all have black bases and the greater number are black throughout. *C. rufilabris* has short, colorless setae, and in *C. oculata* the setae are perhaps as long as in any species seen.

Habits

Where found, and methods of concealment

It is not always easy to find chrysopid larvae. The different species occur in fairly well-defined habitats, and the larvae usually rest extended in crevices of bark, on twigs, on flower clusters, or in rolled leaves. But the somewhat clear body contents of the young larvae blend with the translucent leaves and make the larvae difficult to be seen. Very often they rest on a dead patch in a leaf or in curled-up dried leaves and their predominating reddish color renders them almost indistinguishable.

The most favorable place to search for larvae of *Chrysopa oculata* is on herbage where aphids or young scales are abundant. But even here the larvae are rarely found in numbers. Thirty small larvae of this species were placed on a large stalk of lamb's-quarters which was heavily infested with the black aphids so frequently found on them. The next day a search of five minutes was necessary before the first larva was found. Only three or four were found on the plant, but as many more were found on plants near it.

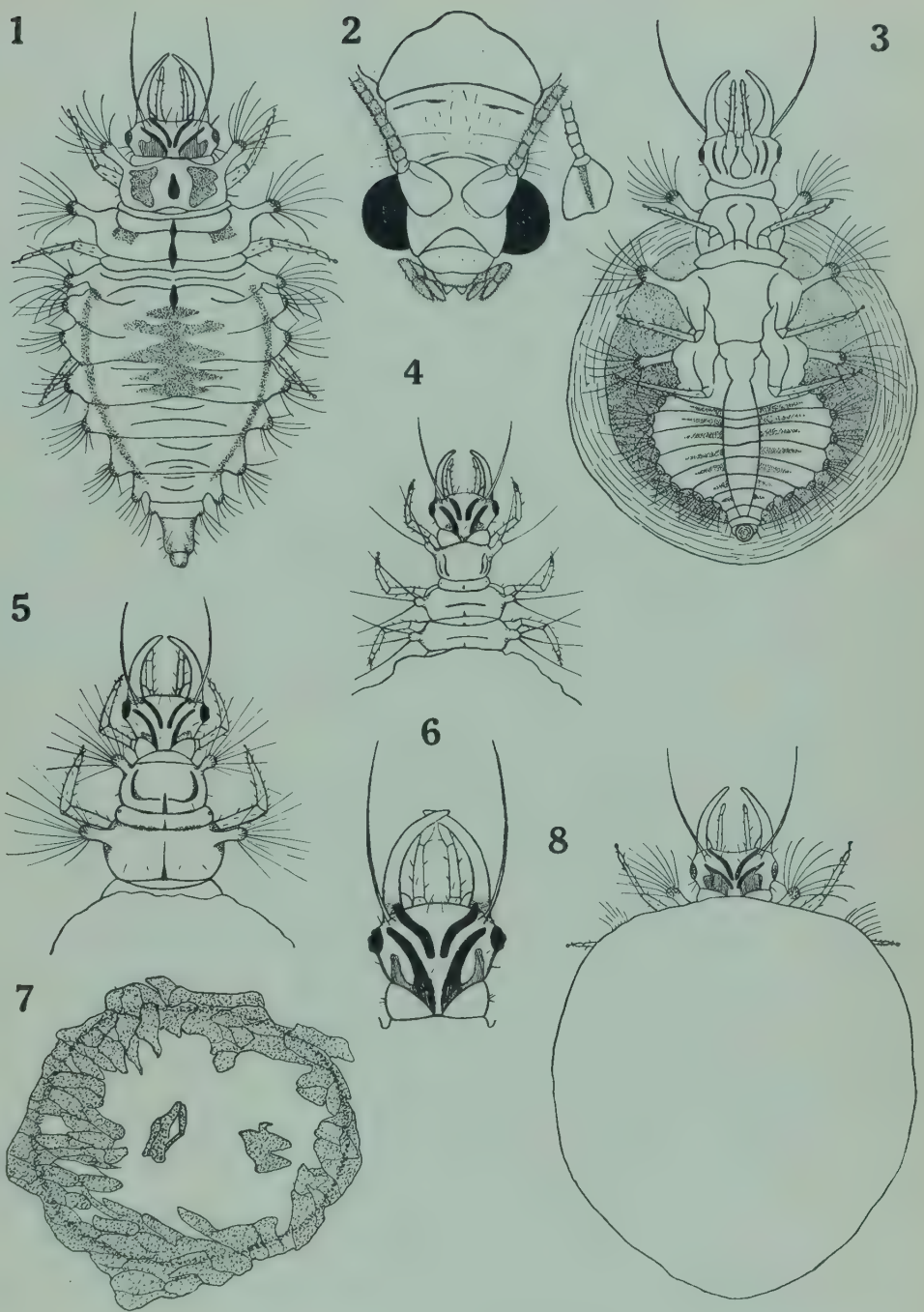
The species frequenting herbaceous plants and shrubs are *C. oculata* with all its varieties (including the two nominal species *chlorophana* and *albicornis), C. rufilabris, C. plorabunda, C. chi* and its variety *upsilon,* and *C. interrupta.* On trees such as the maples that are commonly planted for shade, the chestnut, and the elm, *C. nigricornis, C. rufilabris,* and *C. quadripunctata* are most commonly taken. *C. harrisii* was taken on pine and oak, and *Allochrysa virginica* and *C. lineaticornis* on oak.

Trash-carrying larvae

The trash-carrying larvae of *Chrysopa lineaticornis* have been found on linden trees (on both trunk and leaves), on small oak and hickory saplings, on honeysuckle, and on underbrush in general. They prefer a well-shaded locality. Both *C. bimaculata* and *C. lateralis* were sent to the writer, by state nursery inspectors, from Florida, where they are said to be abundant on citrus trees. *C. cockerelli* larvae were found on the trunks of maple, linden, and apple trees.

The trash carriers build over the abdomen a hollow hemispherical packet.[2] A dorsal view of one of these larvae in most cases reveals no larva at all, but merely a little clump of cottony material, for, when the larva is quiet, the head, the tail, and the legs are drawn in and thus the larva is largely concealed. But when it begins to move, the head and

[2]The word packet is used here because, first, there are many kinds of material brought together, and secondly, the mass is not on the larva's back by accident but is constructed by the larva. It is literally a little pack of debris.



CHRYSOPA LINEATICORNIS

1, Dorsal view of grown third-instar larva, with packet removed; x about 8 1-5
2, Head and prothorax, showing markings; posterior view of antenna showing black line
3, Ventral view of mature larva, with packet in position; x 8 1-5
4, First-instar larva, 5, second-instar larva; x about 10¾
6, Head of third-instar larva, showing third pair of spots
7, Cocoon, showing debris of packet adhering
8, Dorsal view of third-instar larva, with packet in position as in walking; x about 10¾

at least the prothorax protrude anteriorly and the tail protrudes posteriorly (fig. 162, page 1366). The larva walks rapidly and the packet sways from side to side rather unsteadily.

On removal of the packet it will be observed that the larva possesses striking specializations for carrying it. The posterior part is fastened to both the lateral and the dorsal abdominal setae. Rows of minute setae with recurved tips were discovered on the dorsum of the larvae of *C. cockerelli*, and a later study of preserved material of the other trash carriers revealed their presence on these also. In *C. cockerelli* they are more prominent than in the other species, being arranged in from one to three rows across the body from the metathorax to the seventh abdominal segment inclusive. There are as many as thirty of these setae in the longer rows. They are well suited to holding the packet materials securely on the abdomen. The anterior half of the packet is free, but rests on the up-curved, fan-shaped setae of the thoracic tubercles. In addition to the proper support being thus given, the free anterior part permits the larva to stretch out in walking or running. The tail, being free, is extended and so the larva is unhampered in getting about. The abdominal setae are fairly long and the knobs are small. While the abdomen is unusually wide, the segments are narrow, so that the abdomen is shorter and more arched than in other larvae.

The building of the packet is most interesting. The performance may be observed by taking the packet from a larva in a vial, and putting it back into the vial by bits. The larva, with its packet removed, runs around rapidly in evident search of something. With its palpi, antennae, and jaws it seeks from side to side and in every crevice. If a fairly large piece of the packet be dropped into the vial, the larva, touching it, very quickly crawls under it. As soon as the debris is on its back, it is worked backward by the combined efforts of the jaws and a shifting of the abdomen. The head can be bent nearly straight backward when the front pair of legs is lifted, and can be turned to each side for a considerable distance. As soon as the large piece of debris is in place, the larva shifts it from side to side and from the front. A bit of the debris is pulled out and poked back into the pack again. In this way, the material is made more or less solid and the parts are woven into one another to form a firm packet. If more of the debris is added at intervals, it is grasped by the larva's jaws and placed on the anterior border of the packet. It is then worked in and pushed backward, and the straggling ends are picked up and pushed into the packet. Along with the work of the jaws, the abdomen, in a series of wavelike contractions, shifts the packet posteriorly.

Very often the setae, for some reason, catch and hold debris of this nature. Perhaps these setae are more or less viscid. The large cell at the base of each seta has been described as glandular by Lurie (1898), who says furthermore that the setae possess a lumen to the tip. These long setae occur on all larvae, even on species not normally carrying a packet. The dorsal setae are the chief shifting agency. If the abdomen be horizontal and a bit of debris be on one seta, when the abdomen is bowed downward in this region the posterior setae are brought to the packet and will very likely catch into the packet, so that when the abdomen is straightened out the debris will be carried back with the posterior setae. This process takes place in a kind of wavelike shifting, and the packet is actually carried back as far as there are dorsal setae.

After the larva has its packet restored, it remains quiet on a leaf or a twig.

On tearing a packet apart, one finds that it is constructed from bits of debris or small particles of plant tissue which the larva can readily find in its habitat. Insect skins, bits of spiders' webs, egg sacs, the bodies of spiders and mites, bits of wood and bark, lichens, coccid scales and bodies, and insect parts—especially legs, heads, wings (particularly elytra), and antennae—constituted the usual materials of the packets seen. This mass is held together, it appears, by plant fibers, by the silky or cottony secretions of aphids, and by the silk of spiders. The writer found a large amount of such cottony materials accessible to the larvae. Lurie (1898) stated that the packets are bound together by silk spun by the larva. The packets of a few larvae were removed and then returned to the larvae in small pieces. Each larva placed a part of the debris on its back, and gathered up the loose ends and thrust them into the part on its back but did not spin any silk to hold the mass together. The packet is characteristic of all instars, as is true of the Australian species; while silk spinning, in all the larvae observed, is confined to the last part of the third instar.

There are, in literature, statements to the effect that most, if not all, chrysopid larvae put the skins of their victims on their backs as a measure of concealment. The trash carriers are the only ones seen that have this as a well-defined habit. Larvae of *Chrysopa quadripunctata* often carry considerable debris and may appear at times to have this habit, but there is never a well-defined packet present. Larvae of the *oculata* group have frequently been seen with a few aphid skins, or even a number of them, adhering to the setae (Plate LXXXVI, 3). This is to be regarded as accidental, however, or at least as incidental to the larvae's living where there were aphid skins or cottony material, taken with the

fact that the setae are so placed that they readily catch such loose material. Furthermore, it surely is not necessary that larvae be concealed or in any way disguised in order that they may catch insects of such marvelous stupidity as aphids. It is better to interpret this habit as giving security from the larva's enemies, especially birds and hymenopterous parasites, and not as a disguise to assist the larva in catching its food. The trash carriers live almost wholly in the open, as on the branches of trees or the upper sides of leaves. The uncovered species hide in cracks or crevices and in rolled-up leaves which effect similar protection.

Foods

In all species the food of all stages is essentially the same. Very young larvae show a preference for eggs and small aphids or young scales, but they will attack also the larger aphids. Furthermore, if opportunity presents itself, the larvae will attack and kill adults of their own kind. These cannibalistic tendencies, already noted in the case of young larvae, continue throughout the entire larval period. The writer has never observed a larva attack a cocoon and succeed in piercing it. Prepupae and pupae in cocoons appear to be secure from these attacks.

While larvae can thus appropriate their own kind in this manner, their main food consists of small, soft-bodied insects and related forms. Aphids constitute the most important food of all species thus far seen. The larvae of *Chrysopa oculata* ate every kind of aphid given to them. In the main, however, aphids from cabbage, cauliflower, radish, turnips, spiraea, buckthorn, dogwood, maple, chestnut, apple, carnation, chrysanthemum, lily, rose, aster, goldenrod, lamb's-quarters, and nasturtium, were used. All were readily eaten by the larvae. Not all are equally suitable and desirable, however. The most desirable, from all points of view, are the aphids from cabbage, cauliflower (Plate LXXXV, 3), and radish (probably all aphids of the same species), and those from rose. Chrysopid larvae, as well as the adults, attack winged aphids just as readily as they do wingless ones. Where winged forms have been given them alone, they have thrived just as well.

It has been observed frequently that larvae suck up drops of plant juice, and even insert or attempt to insert their jaws into soft plant tissue. Without doubt larvae can derive some sustenance directly from succulent plant tissue.

In addition to eating all kinds of aphids and aphid eggs, the larvae readily attack scale insects. Young scales that have not formed their hard covering are especially suitable for food for chrysopid larvae. If old scales are given to them, they raise the scales or pierce them on the side and suck out the juices. Tower (1915) tells of a Chrysopa larva

which inserted its jaws through the epidermis of a leaf and reached a leaf miner. Walsh and Riley (1868) wrote of a larva which attacked a curculionid larva in a peach. More common are their attacks on small caterpillars, mites, and young or small spiders. Caterpillars larger than chrysopid larvae can ward off the attacks of the larvae by turning the head around or twitching suddenly as soon as touched. Mealy bugs and mites are readily eaten. Small spiders, especially recently hatched ones, are excellent food for young larvae. Marlatt (1895) wrote of attacks of the larvae on the pear psylla. Both adults and nymphs of Psyllidae are readily eaten. Experiments were conducted chiefly with the psyllid species on English ash. A larva of *Chrysopa chi* fed for some time on a much weakened dolichopodid fly.

Chrysopid larvae are not omnivorous. Not all heavily chitinized insects can be pierced by the jaws, and very active insects can be caught only with difficulty. Active larvae, as, for example, fly maggots, frighten away the chrysopid larvae. Coccinellid, chrysomelid, and syrphid larvae, all of which occur in association with chrysopid larvae, are not commonly used for food except perhaps when just hatched.

In the way of artificial foods, beef tea and a weak sugar solution were used. A cotton plug or a piece of absorbent cotton was dipped into the liquid, and the larvae came to the cotton and sucked up the drops. They fed on both these liquids, but whether they could be reared on them was not determined. Both cane-sugar and maple-sugar solutions served successfully for food. The larvae sucked up drops of water also when it was provided.

Larval feeding

The rapidity of feeding, as well as the search for aphids, is somewhat dependent upon how hungry the larva is. When it is very hungry but not weakened, its movements are very agitated and it may even walk over a few aphids without observing them.

After the larva has impaled an aphid, feeding proceeds as follows: The chief movements, as seen from the dorsal side, are the sliding back and forth of the maxillae in the grooves of the mandibles. This is a regular forward-and-backward movement. If both jaws are inserted in the aphid, the two maxillae move together, pulling the labral region backward and forward with it. The aphid is readily turned over and over by spearing it on one jaw, then turning it with the other, and so on, quickly seesawing it back and forth until it is thoroughly exhausted. At the end of the feeding process, the aphid is turned over and over, squeezed out, and finally speared on one jaw. This jaw is moved far outward and the aphid is pushed off the jaw by the tip of the other jaw.

As the larva feeds, the antennae are held almost erect and the labial palpi are held a little forward of straight downward. Undoubtedly in these positions these organs are the least likely to come in contact with the struggling aphid; such contact would either afford some assistance to the aphid in its feeble efforts to get away, or impede the process of turning it over.

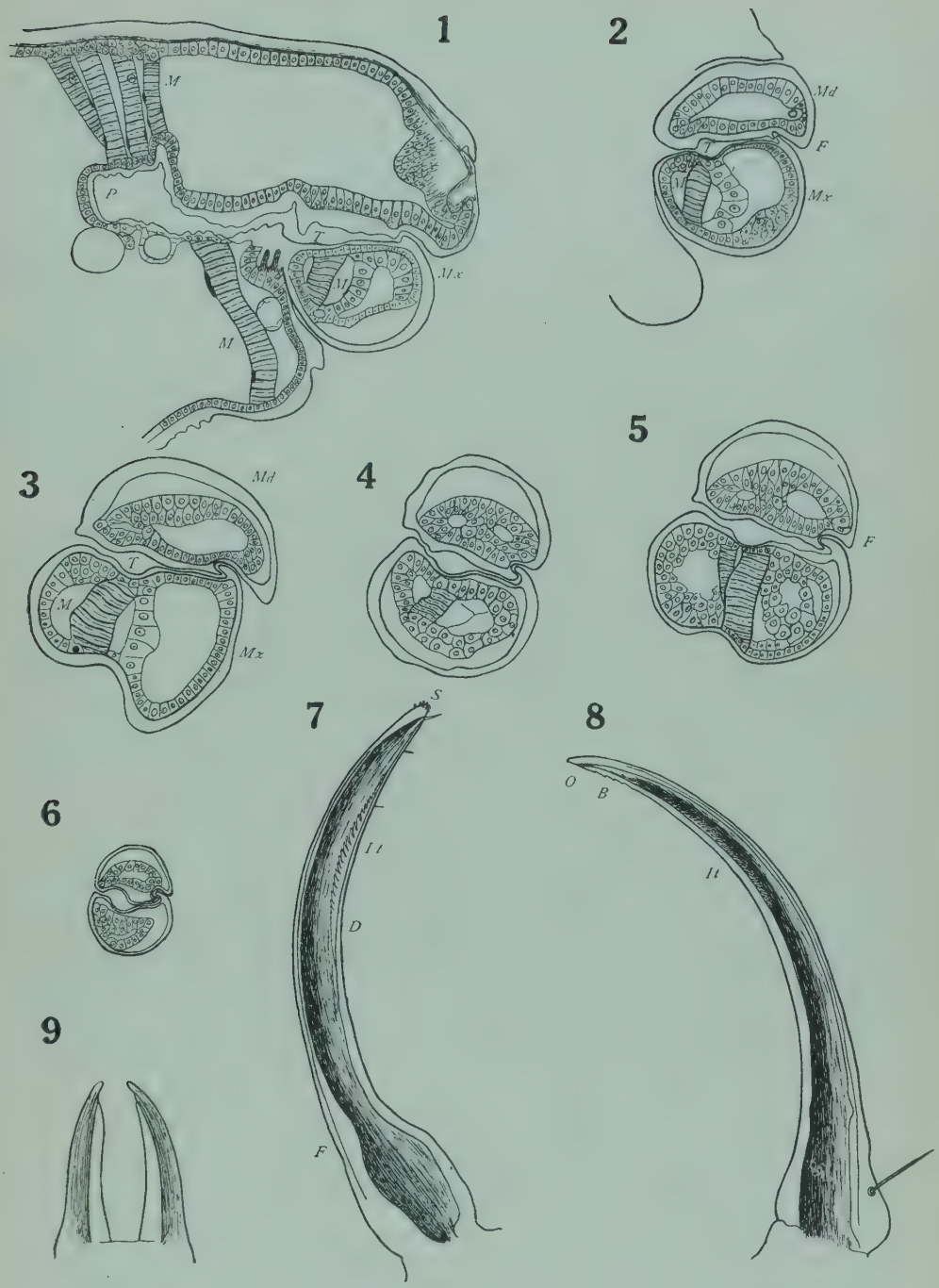
The aphid is nearly always elevated more or less. This is undoubtedly in order to lift the struggling aphid into the air and make its movements futile—not to allow the juices to run down the tubular mouth parts of the larva, as is sometimes stated.

In very young larvae, one can see alternate pharyngeal contractions and expansions near the middle of the head during feeding. This can be observed in newly hatched larvae of *Chrysopa quadripunctata*. Furthermore, if these young larvae are given a small red aphid, a spurt of red juice may be seen flowing into the pharynx with each backward pull on the maxillae. The stream of juices flowing up the tubular mouth parts may be observed also in grown larvae. At the beginning of the feeding, there is generally an uninterrupted stream up each mandible; but as the aphid nears exhaustion, the streams are broken by air bubbles so that their rate of travel up the tubes may be readily observed. When the maxillae are pulled back, these bubbles fly up the tubes very rapidly. At the end of the feeding, only an occasional drop is obtained.

No evidence of the injection of any fluids into the body of the aphid has been observed. The maxillary movement may serve in part to assist in breaking down internal tissues, as these tissues are completely disintegrated, leaving little more than the chitinous parts to be cast aside.

On the ventral side of the head there is more movement visible than on the dorsal. The entire venter of the head, the labium, and the labial palpi, move back and forth with the maxillae. This movement is most evident in the region of the bases of the labial palpi. If only one mandible is inserted, the movement is confined to that side of the venter. The rapidity with which the larva can shift the sucking from one side to the other is striking. First it sucks with one jaw, then with the other, and then with both, more quickly than can be timed.

The muscular action which enables the larva to suck up liquids can be understood by a study of cross sections (Plate LXXVII; also Lurie, 1898). There is a prominent muscle extending from the floor of the maxilla to its upper wall, being attached just beneath the depression that forms the lower part of the sucking tube. This strong muscle is present in all sections from the bases of the maxillae to very near the tips. There is another prominent muscle from the tubular connection of the jaws to



MOUTH PARTS OF CHRYSOPA OCULATA, GREATLY ENLARGED

1, Section through head at connection of pharynx with left jaw (P, pharynx; T, tube between maxilla and mandible; M, muscle; Mx maxilla)
2, Section of jaws beyond head (Md, mandible; Mx, maxilla; F, chitinous flange holding jaws together)
3, 5, 4, 6, In order named, sections of left jaw at intervals toward tip
7, Inner view of left maxilla of a mature larva (S, sensory papillae; It, internal teeth; D, semi-tubular depression; F, flange)
8, Inner view of left mandible. In life this fits above maxilla shown in no. 6. (O, opening into semi-tube; B, apical teeth; It, internal teeth)
9, Jaws of a hemerobiid larva, shown for comparison

the floor of the pharynx. But the most striking musculature is about the pharynx. There is a series of muscles from the pharynx to the dorsum and the venter of the head, as well as to the arms of the tentorium. When these pharyngeal muscles are contracted, the lumen of the pharynx is increased and the juices are sucked up by a typical sucking action. But the muscles in the maxillae also contract and assist the pharyngeal muscles in their work. The opening at the tip of each jaw is single, and is formed by a curvature in both and not in the maxilla alone. The mandibles are sharp at their tips and constitute the piercing agency.

The number of aphids that a larva may eat at one feeding depends, of course, on when it was last fed, on the size of the aphids, and on the size of the larva. A hungry third-instar larva will eat ten cabbage aphids in rapid succession. From ten to twenty larger aphids usually suffice for a day's supply, though more were usually given.

From hatching to pupation, a larva may devour from ninety to two hundred and fifty aphids, depending on their size. The following table is an accurate count of the number of aphids consumed by three larvae of *C. oculata,* by instars, from hatching to spinning:

	Date hatched	Date of first molt	Date of second molt	Date of spinning	Total number of aphids eaten
Larva No. 1	June 1	June 7	June 13	June 18	
Number of aphids eaten, by instars		38	48	68	154
Larva No. 2	June 1	June 7	June 13	June 23	
Number of aphids eaten, by instars		35	68	99	202
Larva No. 3	June 1	June 7	June 14	June 19	
Number of aphids eaten, by instars		46	60	50	156
Average number of aphids eaten by each larva					171

Buckthorn and spiraea aphids were used in this test, and a special effort was made to get aphids of uniform size. At another time a more extensive count was made, using 22 larvae and rearing them through to spinning. In this case 3036 aphids were required, or an average of 138 to each larva. The rather large black aphids on lamb's-quarters *(Chenopodium album)* were used for this test.

Anal proleg of larva

The anal proleg, or tail, is used to excellent advantage by the larva throughout its whole life. It is always used in locomotion except when the larva is running very fast. Then it is either merely lifted from the surface or extended horizontally. In the former case, the abdomen is curved and the end is held just above the surface on which the larva is running. This condition prevails when there is a possibility of the

larva's falling, as in climbing up on the side of a jar or a plant. It is the safety agency in the larva's descent along the stalk after hatching, and it is the larva's main dependence for surety in climbing up and down plants, twigs, glass, and the like. It is used also to brace the body when the larva is handling a struggling aphid.

Reference has been made to a disklike ending of the abdomen. This disk is applied to the supporting surface, and a sticky or gelatinous substance is exuded which enables it to hold fast. At first observation it may appear that the larva holds fast by suction, as stated by Fitch (1855). If a larva be allowed to walk over a fresh, green, smooth leaf, and the highest-power binocular objective be directed upon the tail and the spots covered by it, the little disks of viscous fluid, more or less complete, can be seen on the leaf. It can also be readily seen that the end of the abdomen is immersed in a drop of this clear liquid.

Larval excrement

There is no voidance of larval excrement. It has been known for a long time that the mid-intestine is closed behind (Lurie, 1898, and McDunnough, 1909), and the excrement is stored up in a bean-shaped mass throughout the life of the larva. The darkened appearance of the anterior part of the abdomen is generally due to this black mass within. It is rather surprising that the mass from the entire larval life is so small, but the explanation lies in the fact that the food is liquid and the amount of residue is small.

Classification of larvae

The first basis for classification of the larvae is the marks on the head. These serve to class the larvae into groups which for the most part appear to be most closely related as adults. After the head marks, the general coloration of the body is used. The color of the metathorax varies in the different species. The color of the margins of the thorax and the abdomen are often specific. The first abdominal tubercles differ slightly as to their degree of development. The following key is for third-instar larvae:

A. Two prominent, black, elongate spots on dorsum of head.
  B. Spots extending longitudinally, converging posteriorly.
    C. Jaws amber-colored; legs with smoky or darker patches on femora, but not predominantly dark.
      D. Body of larva brick red or darker above; without a wide gray border on each side of dorsal vessel; yellowish border each side of abdomen; thorax with a prominent yellowish spot around base of each lateral tubercle.....*C. rufilabris* Burm.

DD. Body of larva a more faded red or flesh-colored; a rather large and prominent area of gray on each side of dorsal vessel, leaving a rather narrow dorso-median color area; lateral tubercles of medium size and entirely yellowish or gray..... .....*C. plorabunda* Fitch

CC. Jaws and legs predominantly smoky to black; lateral tubercles small, yellowish; abdominal tubercles 2 to 4 inclusive marked with reddish.....*C. harrisii* Fitch

BB. Spots transverse; anterior one connecting the two jaws, posterior one the two antennae. Larva a trash carrier. Thoracic tubercles much elongated, setae curving upward; abdomen shortened, and bearing a hemispherical packet of debris capable of concealing the larva..... ....*C. bimaculata* McClend.

AA. More than two prominent spots on dorsum of head.

B. Three separate triangular spots on dorsum of head.

C. Metathoracic lateral tubercles reddish, brownish, conspicuously darkened, or black.

D. First abdominal segment having at each side a small tubercle which bears short white setae; second pair of abdominal tubercles gray, often with a trace of bright red; bright red spots on each side of dorsal blood vessel in gray borders of same.....*C. nigricornis* Burm.

DD. First abdominal segment without well-developed tubercles at each side; all abdominal tubercles gray, making a gray border on each side; dorsum of abdomen dark brown or brownish black.....*C. chi* Fitch

CC. Metathoracic tubercles gray or yellowish, in some cases with a small band of reddish above but never conspicuously dark; first abdominal segment without definite lateral tubercles; second pair of abdominal tubercles conspicuously darkened or entirely reddish brown; other abdominal tubercles with slender spot of reddish brown above.....*C. oculata* Say

BB. Four elongate prominent black or reddish black spots on dorsum of head, arranged in two pairs of similar spots; often a suggestion of a third pair by the doubling anterior of outer pair toward the eyes.

C. Abdomen conspicuously short, broad, and somewhat arched, about as long as head and thorax combined; lateral thoracic tubercles unusually long and slender. Larvae trash carriers, normally carrying a hemispherical packet of debris.

D. Inner pair of dorsal head spots stopping near middle of head.

E. Mid-western species; inner pair of head spots confluent behind; area between these spots entirely dark except for narrow grayish area; legs dark; no brown on thorax..... .....*C. cockerelli* Banks

EE. Eastern species; inner pair of head spots not confluent behind, a distinct grayish triangular area between them; thorax generally with light brownish areas dorsally..... .....*C. lineaticornis* Fitch

DD. Inner pair of dorsal head spots extending distinctly beyond middle of head; smoky to black posterior and outer spots; southeastern species .....*C. lateralis* Guér.

CC. Abdomen of the usual type, longer than head and thorax, tapering gradually and regularly posteriorly. Larvae never with well-defined packet of debris, but occasionally with some cottony materials adhering to dorsal setae.

D. Head marks in two pairs, curving outward anteriorly; inner pair V-shaped but not confluent at base; outer pair extending from base of antennae in a sharp inward curve to prothorax; body gray, but marked with brown spots.....*C. quadripunctata* Burm.

DD. Head marks in two pairs but extending straight forward, the two pairs parallel to each other; outer spots twice as large and broad as inner ones; body mainly gray, with prominent black saddle-shaped area on thorax.....*Chrysopa* sp.

The prepupa

After a third-instar larva has reached maturity, it usually seeks a more or less protected place and spins a cocoon of white silk in which it transforms to a pupa. One cannot always tell by the appearance of a larva whether or not it will spin soon. Usually just before spinning, the larva engorges itself by devouring a larger number of aphids than usual and then becomes sluggish. It grows rather broad and usually appears to be somewhat flattened (Plates LXXXII and LXXXVI). The term *prepupa* is used to designate that part of the life stages beginning with the first spinning of silk and lasting until the molt to the pupa.

Location of the cocoon

In the open, the larvae spin on the under side of leaves, at the overturned margins or tips of leaves (Plate LXXXVIII, 4), under roughened bark, in flower clusters, or under loose earth. In vials they usually spin under leaves, twigs, or a mass of aphid skins, near the cotton plug, or on the bottom of the vial. Observations indicate that the greater number go to the bottom of the vial to spin.

It was found that larvae of *Chrysopa oculata* may spin their cocoons just beneath the surface of the earth in pot cages. In nature, cocoons of this species are not commonly found on plants. It is thought that they may go below the surface of loose soil and spin, which would account for their scarcity. The earth and sand adhere to the cocoon and make them quite inconspicuous. Cameron (1913) found that *C. vulgaris* also often pupates below the surface of the ground.

Spinning the cocoon

The early part of the spinning can be readily observed, but the latter part is difficult to see since the cocoon is only slightly trans-

parent. If a larva has been observed as having just started to spin, it may be removed to a glass slide or placed in a cell slide, and after some restlessness it will usually begin to spin a new cocoon. In this way the actual start can be seen. A larva spinning on the bottom of a vial, in the angle, first makes a framework by attaching viscid silk thread from the side of the vial to the bottom. The spinning is done entirely by the tail, which, as previously noted, can be extended and retracted in a remarkable manner. The colorless, gelatinous, silky secretion issues from the anal opening in the center of the tenth segment. The larva lies on its back or on one side, and reaches with its tail in all directions. When the secretion touches the glass, the soft silk readily adheres, forming interesting attachment disks. Then the abdomen is moved over to another place and the silken thread issues as it moves from one place to another. The thread is fastened again, and so the process goes on if supports are located.

But if supports for the thread are not found, the tail searches aimlessly about. Sometimes it seeks in vain and may attach a thread to one of its own setae. The tail can be brought forward over the head of the larva and attach a thread, or it can be twisted to either side to a relatively considerable distance. If no supports are available, the threads are fastened on one side of the larva and then carried up and fastened to a seta, or carried over to the other side and fastened. During the first few hours the spinning proceeds rather slowly, and the more so if much time has been wasted by the larva in seeking places to attach the thread. The larva spins for a few minutes in one position and then shifts and continues in the new position. Threads are attached to other threads and by constantly shifting to a new position the larva keeps the cocoon spherical.

The spinning from thread to thread is carried on in a fairly regular triangular design. The shifting continues at intervals, but instead of shifting in a true circle the larva moves to one side a little, and in this way the wall of the cocoon is made of the same thickness. As the larva shifts, the prominent dorsal and lateral setae are broken off and go into the construction of the cocoon. Perhaps these add a degree of strength and rigidity, like the ribs of a basket. Long before the larva is hidden from view it is without setae.

The spinning continues without cessation day or night unless the larva is disturbed. The triangular design continues until the cocoon is at least half completed. Observation from this stage on is difficult, as the larva is partly hidden. There appears to be a fairly gradual change to a figure-8 pattern. The end of the spinning appears to be a general plastering over the inside of the cocoon, which completely hides the

larva from view. This last act is carried out very slowly. Spinning usually requires from twenty-four to forty-eight hours, though some larvae apparently finish in a shorter time.

Special effort was made to see whether the lid, by way of which the pupa leaves the cocoon, was spun into the cocoon. But to date this has not been seen, nor have any constant characteristics in the spinning process been observed which would warrant the conclusion that it was spun into the cocoon by the larva.

If, while a larva is spinning, the cocoon be torn or the outside be pressed in with a dissecting needle, interesting reactions follow. The larva tries to defend itself and may plunge its jaws through the unfinished cocoon in this effort. Spinning stops for the time being. After a short period of waiting, the jaws are withdrawn and the spinning proceeds. If the cocoon be cut or torn, the opening is patched so that at the end the tear can scarcely be found. It is made of the same thickness as the remainder of the cocoon.

If a spining larva is disturbed, it does one of two things: it either walks around for a while and begins to spin at another place, or goes to the bottom of the vial, coils up, and spends its pupal life outside the cocoon. Disturbed larvae have been observed to come back to the cocoon first begun and spin another beside it. If the first cocoon is well started, the chances are that the larva will not spin further, since, as Lurie (1898) pointed out, the amount of silk secretion is undoubtedly limited, and if too much silk has been wasted in an unsuccessful attempt to form a cocoon the larva cannot secrete enough to complete another. It may, however, spin feebly for about twenty-four hours, making a mat of silk around the tail. A very few larvae appear to make no attempt at all to spin, but pupate in the open.

The cocoon

The cocoon is spherical or slightly elongated in shape (Plates LXXXVII and LXXXVIII), and in all cases pure white in color. The cocoon proper is very thin. It appears like paper, but the original framework gives it more or less of a shaggy appearance. The silky layer is thin, hard, and difficult to tear. It was found, by submerging cocoons for different periods of time, that they could be submerged for several hours without being permeated by water; after a longer time, however, the water did enter. In some cases the cocoon has one or more ringlike bulges. The size of the cocoons varies somewhat in the species, very probably with the size of the larvae that spin them. One cannot with any certainty distinguish the species by the cocoon. The packet-carrying larvae use

their packets as a framework for their cocoons, the debris adhering to the cocoon. The setae to which the debris is fastened evidently break off early in the spinning, permitting the larva to shift its position.

There are two stages in the cocoon—the last part of the prepupal period, and the greater part of the pupal life. The prepupa in the cocoon is doubled ventrad, the tip of the tail lying on the anterior dorsum of the head. It is inactive, but is capable of a little movement. The distinctive colors of the larva largely disappear, but one can usually identify it even after the fading is well advanced. Just before molting, it is often impossible to name the species with certainty. When opened, the prepupa is seen to be filled with a grayish to yellowish white semi-fluid substance, but in the abdomen there is a large, solid, black, bean-shaped body. This is the larval excrement which was packed at the end of the mid-intestine during the larval life. It remains here during the tissue-reforming process through the pupal stage, and the intestine of the adult forms about it.

THE PUPA

The pupa, as it pushes off the old larval skin, is delicate gray to yellowish in color. The eyes are grayish, with small spots of brown. At the center of the base of each eye is a prominent opening, or foramen. The antennae are white or colorless, and are folded over the dorsum of the head, above the eyes, around somewhat to the sides of the thorax, then in an irregular S-like loop over the wing pads, ending behind the wings and somewhat under the body. The most prominent part of the head is the mandibles, which are the most distinctive development of the pupal life. They are relatively large, toothed, and heavily chitinized. Their only movement is as a pair of pincers. There is a prominent labrum. The maxilla and the labium are much reduced but they give a suggestion of the future functional mouth parts. The segments of the palpi, as well as those of the antennae, appear like so many glassy beads. They are incapable of movement. The head is inclined ventrad and its only movement is a slight raising and lowering. The last segment of each tarsus is broadened at the tip, and at each outer angle a very small claw is borne. The wings appear as two pairs of rather prominent pads on the meso- and the metathorax.

FIG. 157. PUPAL MANDIBLES (m) AND LABRUM OF CHRYSOPA OCULATA. X 32. DORSAL VIEW

Color changes and later development

As the pupa develops, the body changes to a distinct bright green. The head, however, retains the yellowish color in most species. The eyes change from a gray to a deep reddish black. As the eyes develop, the retinulae are outlined by little circles of brown pigment forming regular geometrical figures. If these figures be examined under high power, they will be seen to consist of seven rhabdom cells outlined in pigment, with a small, clear, central area. This offers an excellent opportunity to study the gradual deposition of pigment in the developing compound eye.

In the early pupal stage, the head is unmarked, but gradually the head coloration of the adult appears. *Chrysopa oculata* shows very strikingly the dark bands and loops, but *C. nigricornis* does not show the two labral dots at first. These are developments in the early adult. The basal part of the legs becomes light green, while the tarsi remain grayish to translucent. The legs of the adult can be seen developing within the pupal legs, at first faintly but later very plainly. The developing antennae of the adult may also be thus seen. The wings, continuing their growth, soon fill the pupal pads. They then double up, forming regular loops back and forth. This explains how the large wings of the adult can develop in such small pads and be pulled from the pads so easily. As soon as this folding occurs, the tracheation and venation are obscured. The hairs on the wings show clearly and obscure most of the wing surface.

These developmental changes can be followed by the external appearance of the cocoon. As the color of the larva fades to yellowish or gray, the cocoon takes on a tint of the same color. The cocoon, as a whole or in spots, at least after pupation of the larva, has a greenish tinge. In cocoons containing nearly mature pupae, the eyes can often be seen as two dark spots. When these eye spots are the darkest, the green color the most noticeable, and the black disk the most evident, the pupa may be expected to emerge.

Cocoons that were wholly black were sometimes found. This generally indicated that the prepupae within were dead, often parasitized. In cities, black or very dark cocoons were frequently found on trees, but some of these had been discolored by soot or smoke. Fungous growths on a cocoon have been observed to be positive evidence of the death of the pupa or the prepupa.

Length of pupal life

The shortest periods of time from spinning to pupation in the different species was from three days to twelve days. Records of from ten to twenty days were more frequent than earlier ones. In overwintering generations, which remain in the cocoon as prepupae, this molt does not occur for a period of from four to eight months. The pupae emerged from the cocoon in a minimum of five days after pupation. This gives a minimum of eight days in these rearings for the length of pupal life. Records of from twelve to twenty-five days, however, were more frequent. Development was most rapid in midsummer.

Emergence of the pupa

When the pupa has matured, it leaves the cocoon through a circular opening at one end. This opening is generally directly opposite the black disk, though in rare cases this disk, which is the molt, may be located on the side. The pupa, by exerting sufficient upward pressure, causes the end to tear in the form of a circular lid, which was observed in all cases to be hinged by at least a few threads.

A question has arisen as to the exact manner in which this lid is formed. Some writers state that it is spun into the cocoon, others that it is cut free from the cocoon by the large pupal mandibles, and still others that it is torn by upward pressure. The writer has not observed anything at spinning that might be interpreted as the formation of this lid in any species. If it were cut by the mandibles, it appears that the edges might be jagged and somewhat irregular, yet this is not the case. Furthermore, cocoons would occasionally be found with the jaws protruding in the act of cutting the lid, yet this has been neither seen nor reported.

The writer is not definitely convinced as to the correct explanation. It appears most likely to be a combination of the above explanations. The cocoon is so constructed that, when a rent is started, it tears in a circle with clean edges. Near the ends, one can tear off a lid; near the middle, however, the ends of the tear do not meet, but a narrow strip like a continuous apple peel results. Therefore the manner of spinning may account for the end tearing in the form of a lid.

It has been repeatedly observed through the thinner cocoons, as of *Chrysopa rufilabris* and *C. plorabunda*, that the pupa is able to shift its position with surprising rapidity. This can be demonstrated by exerting a little pressure on the exterior of the cocoon. The pupae have been observed to turn quickly to avoid injury. By raising its head slightly, a pupa can bring pressure to bear on the upper end of the

cocoon. It is possible that by the shifting about of the pupa in the cocoon, some area is weakened, so that when the pressure is exerted the rent begins. However, no observations have been made substantiating this theory. After the rent has been once started, the further pressure and emergence of the pupa causes it to broaden to almost a circle.

Once out of the cocoon, the pupa must molt before it becomes an adult. This molt was the critical period in reared Chrysopidae; the fatality in these rearings was at first between thirty and sixty per cent. It was observed that as soon as the pupa had emerged, it walked around on the bottom of the vial and sought repeatedly to climb up the sides. When twigs or leaves were placed in the vial, the pupa climbed up at once, holding on with its claws and occasionally using its jaws to assist it. After hastily investigating the leaf or twig, the pupa braced its legs and began the stretching and expanding process which makes possible the splitting of the pupal skin. The providing of materials enabling the pupae to climb and properly orient themselves greatly reduced fatalities. If suitable supports are not found, the pupae may not be able to molt, but may grow weaker and more inactive and finally die. A weakened pupa rarely succeeds in shedding the pupal skin, as the process is a strenuous one, requiring all the strength that the most active pupa can exert. Pupae may also be removed to plants, where the molt can take place under natural conditions.

The pupal molt

The shedding of the pupal skin corresponds very closely to a larval molt. The writer has frequently watched pupae shed their skins, under a lens, and one instance, that of a female of *Chrysopa oculata*, may be described as a typical case.

The pupa emerged from the cocoon and was taken from the vial and placed on a plant. It walked around over the leaves excitedly, and thus investigated several leaves. Finally it took up its position near the end of a stem. It braced its legs and began to inflate or expand itself by a series of regular movements simulating breathing. Numerous writers have commented on the phenomenon of so large an insect coming from such a small cocoon; in fact, the size of the expanded pupa is several times the size of the cocoon. The abdomen is extended to the normal adult length. The thorax also is expanded. There is considerable muscular movement during this expansion. The abdomen is raised and lowered, and extended and contracted, alternately. The head is raised and lowered. This pupa continued the expansion for ten minutes. It rested for perhaps a minute, and then a series of movements, calculated to shift the abdomen forward, was begun. The abdomen and the thorax

moved forward within the pupal skin, leaving it behind. The inevitable consequence was the stretching of the pupal skin in the anterior region. This continued until a rent started. There has been some difference of opinion as to just where the tear occurs. In this instance, it began over the occiput of the head and was rapidly extended back over the prothorax by a few further shifts. Bending the head caudoventrad, the pupa first carefully freed its mouth parts. It pulled upward and worked the mouth parts constantly. The antennae formed two loops over the front of the head and began at once to slip out of the old pupal skin. The pupa pulled upward slowly and deliberately on the mouth parts, continuing to move them in and out. Finally they slipped off, revealing the bright colors of the head. The pupa then began to straighten up slowly in order to pull out the antennae and the two anterior pairs of legs. The antennae were guided upward by the maxillae. These were spread apart and they grasped the antennae in the withdrawing process. The metathoracic coxae may also assist in the withdrawing of the antennae by being moved forward and pushing the antennae outward.

The pupal skin remained attached throughout this performance. The pulling upward continued until the pupa appeared to be supported only by the abdomen. Finally the front legs were freed, followed by the second pair. At about the same time the antennae were free and sprang into place. During this performance the wings were pulled from their pads. As the adult lifted itself upward, the chitinous linings of the tracheae were pulled out. With the freeing of the anterior part of the body, the pupa, having the first two pairs of legs free, walked slowly ahead, thereby pulling out the metathoracic legs, the remainder of the wings, and the end of the abdomen.

The pupal skin remained attached as a hyaline molt, retaining its former shape but with a large rent above and possessing no characters by which the species could be determined. Two long, slender claws at the end of each tarsus could be seen, but the pulvillus was not well defined.

Very little variation from the foregoing account has been observed in the different species studied. In *C. nigricornis* the rent was observed to be started at the border between the meso- and the prothorax. It then extended forward to the head, and continued to the eyes in the form of a Y. The whole process, from the beginning of the expansion to the time when the adult walks away, requires from fifteen to twenty minutes.

THE ADULT

Expansion of the wings and darkening of the veins

The imago generally walks about excitedly for a few seconds, going a short distance and then coming to a stop with the end of the abdomen downward. This position facilitates the spreading of the wings. If the supporting surface be turned upside down repeatedly, the imago will just as often assume its first position. The wings expand presumably by blood pressure, the expansion beginning at the base and extending outward. The tips are the last to expand, usually requiring a half hour before being fully expanded.

The veins and veinlets of the wings are wholly green at first, but certain ones soon begin to darken, first at the basal part of the wings and lastly at the outer parts. The adults of *Chrysopa oculata* exhibit a variation in this respect, from entirely green to fairly dark. A series may readily be arranged, including perhaps twenty individuals, with a gradual succession of changes in the extent of pigmentation of the veins. *C. nigricornis* also shows considerable variation. The first veins to darken are the gradate series, between the branches of the radius. The costal veinlets and the ends of the branches darken next. The base of M_{3+4} (the divisory veinlet) has not been observed to be a true index to the degree of darkening of the wing.

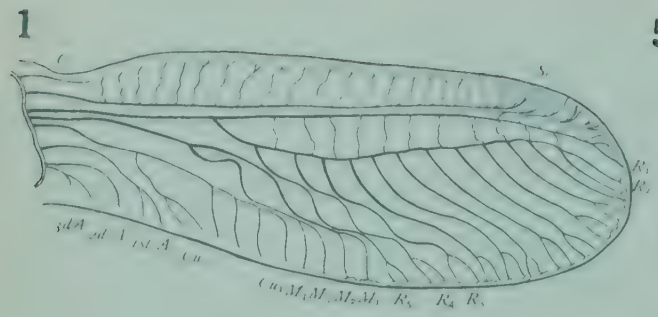
Voidance of larval excrement

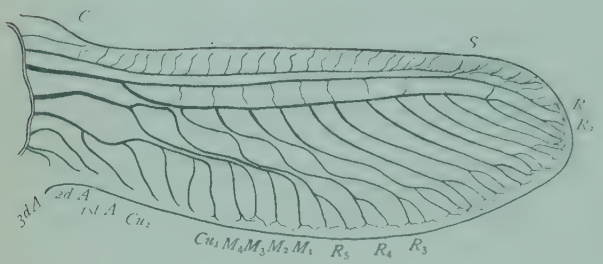
The black mass of larval excrement which was seen near the end of the abdomen of the pupa, and which, in the newly emerged adult, can be readily located, still must be voided. The voidance appears to require considerable effort, and is accomplished from five to fifteen minutes after the wings are expanded.

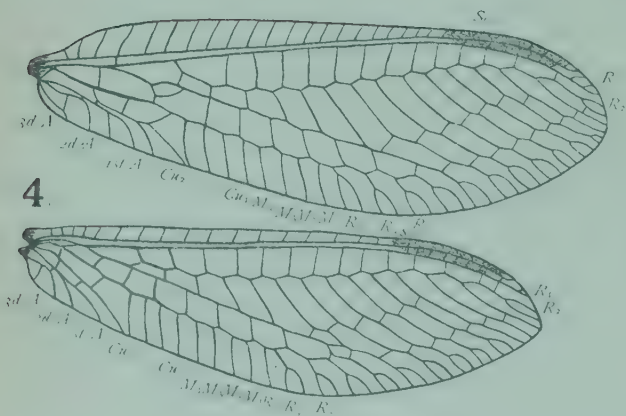
Tracheation

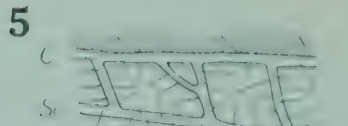
Pupal tracheation

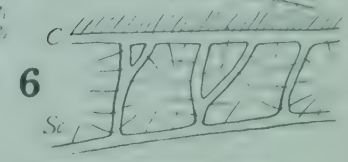
The camera-lucida drawings of the pupal tracheation (Plate LXXVIII) show clearly its essential points. The costal trachea appears as a very short and rather indistinct trachea at the usual place. It has been overlooked by other workers, but in the course of these studies it has been seen repeatedly in *Chrysopa oculata* and *C. nigricornis*. The branch M_1 is so close to R_5 that it appears to be a part of the latter. Tillyard (1916-17) has so interpreted it in *C. signata,* but in both *C. oculata* and *C. nigricornis* it is clearly a medial branch. A similar condition exists in the cubital region. The outer branch of the cubitus appears super-

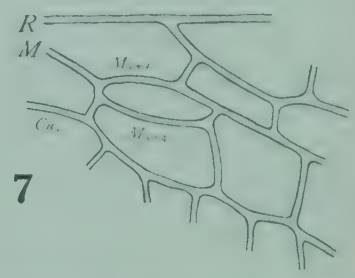


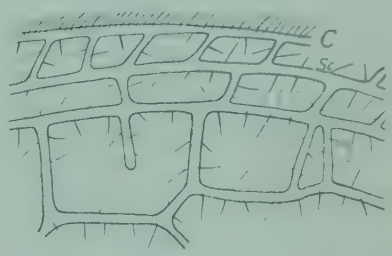


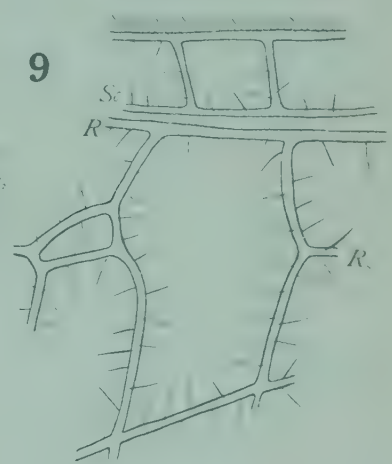












WING VENATION

1, Front wing, 2, hind wing, of early pupa of Chrysopa oculata. x about 10¾
3, Front wing, 4, hind wing, of C. nigricornis
5, Branching in subcostal veinlet of wing of C. oculata. 6, Branching in subcostal veinlet of another wing of C. oculata. Both x about 18
7, Unusual fusion of M_{3+4} with M_{1+2} in wing of C. oculata. The so-called divisory veinlet is here very similar to that in Allochrysa)
8, Accessory veins between R1 and Rs in region of stigma of C. oculata. x about 18
9, Dropping-out of Rs in hind wing in C. oculata, x about 18

ficially to be a branch of the media. This branch sends three smaller branches to the outer margin. The fourth branch basad is Cu_2. There are usually only three anal tracheae, but in several instances a minute fourth was seen. There appears to be some variation in the second and third anals. These tracheae are small and difficult to study, but the essential features are fairly clear. The tracheation of the hind wing is almost identical with that of the fore wing.

Application of tracheation to wings of adults

It is evident that a correct interpretation of the venation of the adult Chrysopidae is impossible without a previous understanding of the pupal tracheation. The modifications shown are peculiar to the family, so far as is known. The first modification is seen at the tip of *Sc*. In the pupal wing, *Sc* ends at the inner border of the stigma. In the adult wing it appears to end beyond the stigma and near the tip of the wing. The stigmal cross-veinlets are the fused branches shown in the pupal wing from R_1. There are few cross-veins between *Sc* and *Rs*, and these are at the extremities. This condition enables a kind of rotation to take place in flight, for both the cutting edge of the wing and the flexible hind border. The radial sectors in both pairs of wings of the adult are zigzagged, while in the pupal wings they are straight tracheae.

It is at the end of the radial system and throughout the medial and cubital systems that the greatest coalescence occurs. The best way to name these branches is to find Cu_2, which corresponds to that branch in the pupal wing. It arises rather far basad from Cu_1, and is branched in the front wing and unbranched in the hind wing. This vein having been found, the fourth branch forward is Cu_1 in both wings. Then, in regular sequence forward, the veins are M_4, M_3, M_2, and M_1. It will be observed that in both front and hind wings this arrangement generally holds, stopping with the fork of R_5. In either wing, however, some variation occurs in this region. M_1 and M_2, and M_3 and M_4, may be joined at their bases and simulate the branched R_5. M_1 may also be branched like R_5.

The branches having been named, they can be traced to their origin. The ninth radial branch from *Rs* is the last to go straight to the margin without fusions. The tenth to the fourteenth branches, inclusive, so fuse at their bends as to form the pseudo-media and the pseudo-cubitus. *M* is fused with *R* at the base. In the front wing it divides into two branches which fuse quickly, forming the median loop and then separating. Apparently there may be considerable variation in the median loop. The lower branch, M_{3+4}, shifts along the upper branch and may

even fail to fuse with it, as shown in Plate LXXVIII, 7. In such a case a very evident specimen of *Chrysopa oculata* might be placed in the genus *Allochrysa* by existing keys. A specimen of *C. rufilabris* was observed to entirely lack a median loop in one wing. But these variations are unusual, and in the great majority of specimens the wing-venational characters used by Banks and others in keys may be relied upon.

In both wings, *Cu* arises as a separate vein. Soon after its origin in the front wing, a marked thickening occurs. There is nothing in the pupal tracheation that explains it. Cu_2 arises at this thickening and runs toward the margin, but branches slightly beyond half the distance to the margin. The main vein continues forward and gives off four branches to *C*, the anterior of which becomes Cu_1. This differs from Tillyard's interpretation, in that he has shown only three branches from the anterior branch of *Cu* to the margin, compensating by calling R_5 three-branched at the tip.

The short crossveins connecting the radial branches have been designated as gradate veinlets. The various genera differ as to whether there is one or two series present, and also as to the number in each series.

Foods

There has been some difference of opinion expressed in the literature on the Chrysopidae as to whether or not they take food. From the beginning of these studies, *Chrysopa oculata*, *C. nigricornis*, *C. rufilabris*, *C. quadripunctata*, and *C. chi*, were fed plant lice daily, which they ate very readily. The first two species listed were observed to eat them in their natural habitats. Any small aphids, young scales, and mites that happened to be available were given the chrysopids, and were readily eaten though not all were equally suitable in rearing work. A hungry adult of *C. oculata* was observed to devour seven cabbage aphids in succession. All adults apparently relished some water daily also. On the other hand, *C. plorabunda* was never observed to devour live aphids, though this species fed freely upon fluids of crushed aphids, weak sugar water, and plain water. Similar observations were made with *C. harrisii*, *C. lineaticornis*, and *Allochrysa virginica*. While these were offered various aphids, they were observed to feed only upon sugar water and water. It is thought that the proper food was not discovered, or that the insects may have fed during the night, rather than that they normally took no food.

It can be readily observed that adults depend largely on tactile sensations, rather than on sight, to locate their food. The palpi are

largely used for this purpose. Aphid skins and dead aphids call forth responses similar to those called by live aphids. When the live aphids are encountered, their movements are readily detected, and then they are quickly seized and devoured.

Flight

The flight of the adult is slow, heavy, and rather awkward. The wings are large and the body is comparatively heavy. In the sun, the light is reflected by the wings but the usual color impression is green. Although the flight of the chrysopids is distinctive, they are frequently confused with some Plecoptera (especially Chloroperla), Mecoptera, Hemerobiidae, and the smaller Lepidoptera.

Activity of adults

The inactivity of the adults during the day has been commented on by many writers from Réaumur to the present time. The insects prefer to remain quiet on trees, shrubs, and herbs, during the day, and fly chiefly in the morning and evening. They sit probably most often on the under side of the leaves. Sweeping and beating are the most successful means of taking them during the day.

At Ithaca and at Milwaukee the greatest activity was manifested in the evening, as was evidenced by the attraction of the adults to the electric lights, especially arc lights. It was found that a better collection could be taken here in a few hours on a favorable evening than in several days of sweeping. The activity of the adults begins early in the evening, perhaps at seven o'clock in summer, and their numbers increase until about nine or ten o'clock. The greatest numbers of adults on the wing have been observed on warm, still summer evenings. If a rain be nearing, the conditions are still more favorable. In Virginia, though frequent watches were made at lights, comparatively small catches resulted and nothing rare was ever taken. Adults are somewhat attracted also to sugar put out for moths at night.

Cleaning the antennae and pulvilli

An interesting performance seen frequently in adult chrysopids is the cleaning of the pulvilli and the antennae. The right antenna is cleaned by the right front leg. The tarsus is looped over and the antenna is drawn through the loop. The long hairs on the tarsal segments serve to remove attached debris. The left antenna is cleaned by the left tarsus in the same way.

When an adult attempts to climb up the side of a glass bottle, the pulvilli must evidently be very clean if it is to succeed. The pulvilli are cleaned by the mandibles and the maxillae. The insect picks off adhering particles and apparently bites the pulvillus, probably to increase the flow of adhesive material. All the legs are cleaned by being drawn through the mouth between the maxillae and the labium, the right legs being drawn through the right side of the mouth and the left legs through the left side. There seems to be an adjustment for this in the mouth parts, as there is a definite space, apparently well suited to the purpose, between the maxillae and the labium.

Protective devices

The color of the adults so closely simulates their environment that considerable protection is afforded. But more striking is the repellent odor of most species. This odor is sickening and very objectionable, and has been described as resembling that of human feces. McDunnough (1909) gives a brief account of the glands secreting the fluid that produces this odor. The odor appears to vary in intensity between the individuals of the different species, but it is generally strong in the *oculata* group, in *Chrysopa chi*, and in *C. nigricornis*, and weaker in the *quadripunctata* group. The full strength of the odor may be demonstrated by slightly squeezing the body of an adult between the fingers. A mutilated specimen gives a similar result. The odor will persist on the hands for several hours after adults are handled. This odor is only a partial protection from the insects' enemies, though predacious enemies have been observed to be less serious than parasitic ones.

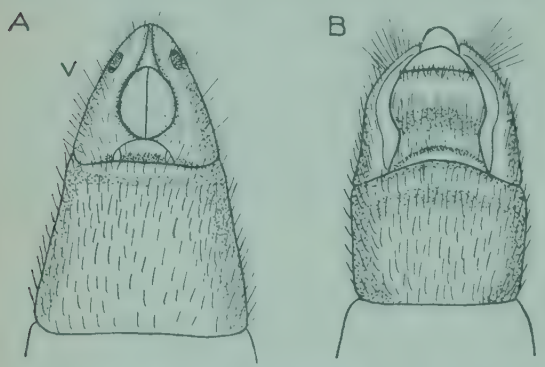


FIG. 158. END OF ABDOMEN IN CHRYSOPA OCULATA, X 8. VENTRAL VIEW

A, In adult female. The two circular areas of peculiar setae are shown, also the genital opening (v)
B, in adult male

The sexes

It was early noticed that the egg-laying females nearly always have very much distended abdomens, due to the eggs contained. So when adults are taken with abdomens larger than normal, it is generally safe to call them females. But the sexes have constant differences in the external genitalia which readily distinguish them.

The end of the abdomen of a female of *Chrysopa oculata* is

seen to be made up of two prominent side lobes, which meet at their posterior extremity but are separated anteriorly (fig. 158, A). The very prominent oblong vulva is located between these lobes, at their base. It has a sharply defined border and is not covered with the prominent hair seen on the lobes. A suture running from in front posteriorly divides it into two equal parts. Both the gelatinous stalk-forming substance and the egg issue from this opening at oviposition.

A ventral view of the end of the abdomen of a male of *C. oculata* shows marked differences from that of the female. The two lateral lobes stop short of the midline and a prominent ventral plate extends between the two borders (fig. 158, B). This ventral plate has a prominent depression extending across it near the middle. There is another lesser depression, parallel to this and a little posterior to it. This ventral plate extends practically as far caudad as the lateral lobes. The genital opening is within the extreme end of the abdomen, above the ventral plate, and the anus opens above it. In side view the abdomen ends squarely, in contrast with that of the female, which has a rounded end, the dorsal part being longer than the ventral. The depressed button-like circular areas bearing the short, peculiar setae occur in the males as well as in the females, one on each side near the dorsum.

Sexual dimorphism

In addition to the genital differences, there is a striking sexual dimorphism in *Meleoma signoretti*. The male develops a prominent frontal horn, which bears a brownish ventral brush of hair (Plate LXXXIV, 6). In the male of *M. slossonae* there is a suggestion of this development and the surface of the front is somewhat irregular, but a definite horn is absent. McLachlan (1883-84) discussed a difference in the width of the costal area of the wings in the two sexes of *Chrysopa flava*.

Copulation

Copulation has never been described for the Chrysopidae. It has been observed several times in *Chrysopa oculata* and *C. nigricornis* during these studies. As a typical case, copulation of *C. oculata* observed under a binocular on June 26, 1916, may be described. About half a dozen pairs of adults of *C. oculata* emerged on June 24. They were put in a battery jar, which was then placed upside down over a small plant infested with aphids. At about 4.30 p. m. on the 26th, several females appeared to be chasing the males about. When they came near each other, both the males and the females began to jerk the abdomen upward

and downward, an act which is generally seen before copulation. The males and the females rubbed their antennae together, and usually the males would fly away. Finally a male and a female continued stroking each other vigorously with their antennae. Then they walked to a position beside each other, facing in the same direction. Then they moved their abdomens together, the male bringing his under that of the female so that the ventral surfaces of the two were together. The male held the abdomen of the female securely. Later they headed in opposite directions. Connection continued for twenty-eight minutes. During this time the only perceptible movements were a slight waving of the antennae and contractions of the abdomens resembling slow peristalsis. Finally the female became restless and started to fly away, but the male held her, even supporting her suspended. After several further efforts by the female to break loose, they separated. Each brought its abdomen forward and appeared to be eating at the genitalia. The male held his genitalia open for five or ten minutes after copulation.

All other cases of copulation observed also occurred at about four or five o'clock in the afternoon. A pair of *C. nigricornis* copulated at least twice. They emerged on successive days and were put together immediately. The female laid about two dozen eggs, which hatched. After these eggs were laid the insects were found in copulation. The beginning of the copulation was not observed, but the insects remained in connection for a half hour from the time when they were first observed. After this copulation, several dozen more fertile eggs were laid. The evidence of the first copulation was circumstantial but, since fertile eggs were deposited, it is not likely that the supposition was ungrounded. The second copulation was observed.

Egg-laying after copulation

A number of experiments were carried out to determine the length of time that elapsed after copulation before the first egg was laid. The female whose copulation is described above, began laying eggs the day after copulation. Observations show a varying lapse of time, from a few hours to six days. The females are fertilized generally soon after emergence, but a minimum of three days is required for the eggs to develop. If oogenesis is well advanced, fertile eggs may be deposited very soon after copulation.

It was observed in several instances that in *Chrysopa oculata*, eggs formed when the females were unfertilized. The females deposited a number of unstalked eggs in the vials, as well as some stalked ones which failed to develop embryonically. A female that had deposited unstalked, infertile eggs, after copulation deposited stalked, fertile ones.

Manner of oviposition

The stalked eggs of the Chrysopidae early attracted attention, and the manner of oviposition has been correctly described, at least in the main, by several writers, notably Fitch (1855), Mueller (1872-73 a), Vine (1895), and Girault (1907 a).

Oviposition has been observed many times by the writer both under a hand lens and under a binocular. A female with a much swollen abdomen may be expected to oviposit soon. Furthermore, if a female is seen to have very recently deposited a few eggs, oviposition may generally be observed without a long wait on the part of the observer. There is a constant twitching and contracting of the abdomen preceding oviposition. Rings of contractions run posteriorly, and the abdomen is repeatedly raised and lowered. The female is usually quiet, moving only when disturbed. The vulva becomes more prominent, then it bulges out, and immediately before oviposition it is pushed out to its limit, being then very conspicuous. Finally the abdomen is brought to the substratum once or several times. Then it touches the substratum apparently with more force, and a drop of clear gelatinous substance is exuded. Following this exudation, the abdomen is raised stiffly upward. The gelatinous substance is pulled out in this way into a long, fairly uniform stalk. Immediately the egg appears, micropyle end last, and attaches itself to the stalk. The egg is held for an instant, presumably while the stalk hardens.

It was observed that the egg in many instances was held not by the genitalia but by the small amount of stalk material which adhered to it. When the drop of gelatinous material appeared, the genitalia were immersed in it before it was drawn out. The egg adhered to it and was held for a few seconds. If the abdomen was lowered a trifle, the stalk bent out of line. After the stalk hardened, the adult freed itself from the egg with a little jerk. Some of the gelatinous substance was frequently seen on the eggs.

The females of the less common species refused to oviposit in captivity, though several types of containers and foods were used. It should be pointed out further that some exotic chrysopids normally deposit unstalked eggs, but all of our species thus far studied normally deposit stalked eggs and all oviposit in the manner described.

Abnormalities in oviposition.—Various peculiarities have previously been described as accidents of oviposition. In closely grouped eggs, as are frequently found with *Chrysopa nigricornis*, striking abnormalities may be observed. Most species deposit their eggs singly, but Sharp (1895) reports *C. aspersa* as laying its eggs in groups, each group being supported by a single stalk.

Not infrequently stalks without eggs were found, also a stalk with a small part of an egg on it. A female of *C. nigricornis* which had demonstrated these and other abnormalities was watched one afternoon. Oviposition was repeatedly attempted, though it appeared that the eggs had become lodged. The insect was observed to deposit a half dozen stalks without eggs, also some stalks with small pieces of the chorion on them. She also deposited other pieces of chorion indiscriminately without stalks. She later deposited normal, stalked eggs. She also deposited one stalked egg with an unstalked egg adhering to it (fig. 159, B), and another with a piece of chorion attached to a normally deposited egg. Near the end of her life she deposited a few fertile eggs without stalks.

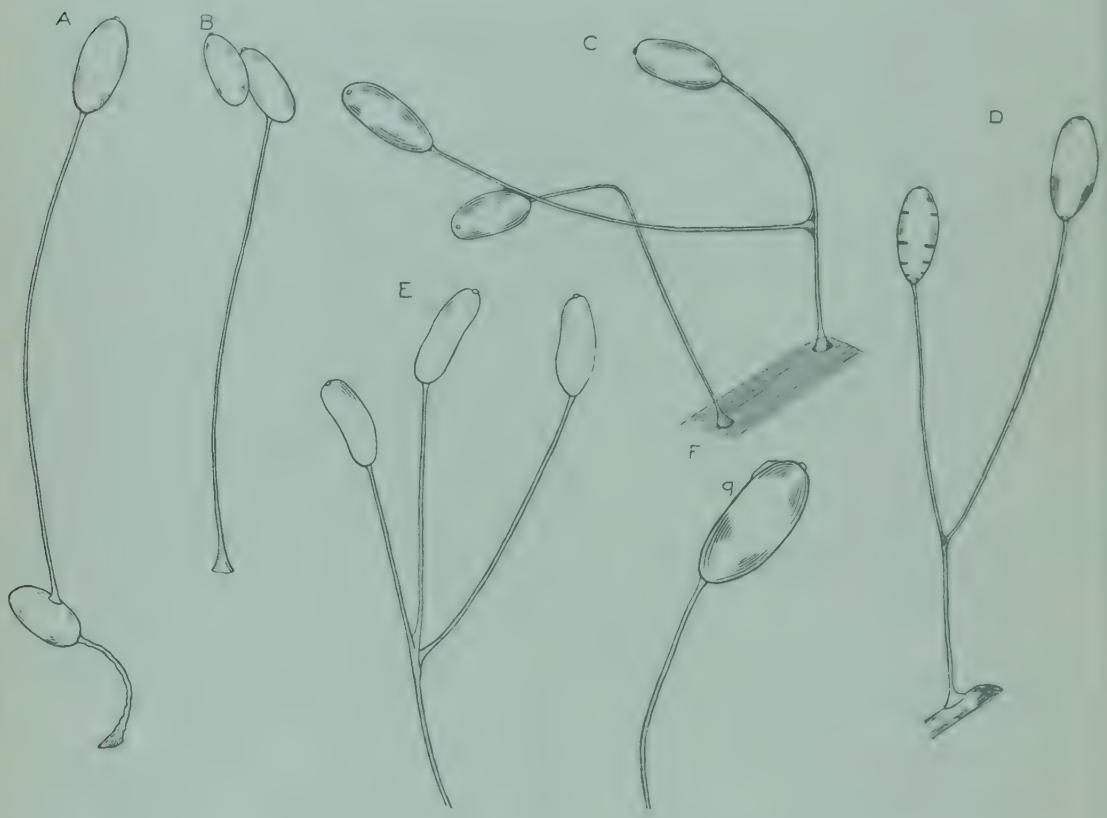


FIG. 159. ABNORMALITIES IN OVIPOSITION

A and B, Abnormal oviposition in Chrysopa nigricornis, x 5¾. C, Accidental fusion of stalks in C. oculata. D, Abnormal oviposition in C. chi. E, Abnormal oviposition in C. oculata. F, Egg of C. oculata showing a drop of the gelatinous stalk material (g)

Length of oviposition period and number of eggs laid.—The usual statements on the length of the egg-laying period are that the adult is short-lived and that oviposition lasts for only a few days. Great variation occurred in rearings, undoubtedly due to the fact that few if any females deposited their full complement of eggs. The largest number of eggs obtained from any one individual was 617, from a female of *Chrysopa oculata* which lived for forty-two days. The second largest number was 470, from a female of the same species which lived for thirty-four days. There was but one copulation in each case and no infertile eggs were noticed. In both cases egg-laying continued up to the day preceding death. Female No. 63 of this same species deposited 326 eggs and then died. On opening the abdomen, 13 nearly mature eggs were seen. Other records in this and other species were in the main smaller than the above numbers, ranging from 294 to 0. The number of eggs that can be deposited is evidently larger than has been previously reported.

Length of life

There is considerable variation in the length of life of different individuals. During an attempt to winter adults, a female of *Chrysopa rufilabris* lived for eighty-one days and a male of *C. quadripunctata* for fifty-nine days. The periods given in the preceding paragraph are the longest records for females of *C. oculata,* while the longest record for a male was thirty days. Adults of this species usually lived for two or three weeks in rearings, but the less common species, as *C. harrisii, C. lineaticornis, Allochrysa virginica,* and the species of Meleoma, could not be kept alive longer than a week, or at most ten days. Adults of *Chrysopa plorabunda* have been kept alive from October to April, but during the summer have not remained alive for more than three weeks.

NUMBER OF GENERATIONS IN A YEAR

The number of generations varies with the different species and with the latitude. A pair of the species *Chrysopa oculata* emerged in the laboratory on February 18, 1915, and by July 1 four generations had been reared. From fragmentary outdoor rearings and collections, there are apparently three generations of *C. oculata* in New York and four in Virginia. There are very likely four generations of *C. plorabunda* in Kansas, but only two of *C. cockerelli.* There are two generations of *C. lineaticornis* in Virginia, but collections would indicate only one of *Allochrysa virginica.*

HIBERNATION

The majority of the species of Chrysopidae winter as prepupae within their silken cocoons. It is usually stated that they winter as pupae, but by opening cocoons monthly during the winter, it was found that they remain prepupae. *Chrysopa plorabunda* normally overwinters as adults in Kansas. In the mild winter of 1920-21, this species was active almost all winter and could be taken in numbers on warm, sunshiny days. During the more severe winter of 1921-22, none could be found flying in the open nor caused to fly up by beating. *C. interrupta* was reported by Banks (1915) as hibernating at Mount Vernon. Adults of *C. vulgaris* have been reported by McLachlan (1869) as wintering in a hornet's nest. *C. flava* has been reported by several writers as wintering in the adult stage.

One species, *C. cockerelli*, was found to winter as practically grown larvae. Larvae of this species were kept alive over winter without food in an attic and in a cave. Furthermore, an overwintering larva was found on April 4, 1921, in an apple orchard under a piece of bark. In the South, Chrysopidae breed continuously through the year.

Repeated attempts to winter eggs, larvae, and adults of species other than those previously mentioned have failed. Adults of *C. rufilabris*, *C. quadripunctata*, and *C. harrisii* were kept alive until November and December in Virginia in outdoor protected cages, but they finally all died. Immature larvae of our common species die if they are not fed, and when they are fed they go on to maturity and spin cocoons in which they winter as prepupae.

During the winter cocoons of the tree-inhabiting species may be found in crevices of the bark on maples, oaks, and elms, on leaves in heaps along hedgerows, and in similar protected places according to the habits of the larvae.

Discoloration in hibernating adults

Overwintering adults are usually much reddened, and their green color is largely replaced by brown as a result of the cold and from lack of food. Banks (1915) reported discoloration in *Chrysopa plorabunda*. Kolbe (1893) stated that the green color of chrysopids was due to chlorophyll, and ascribed the color change of *C. vulgaris* in the fall and after death to factors causing a comparable change in the leaves in autumn.

Specimens of *C. rufilabris* taken at Milwaukee on September 27, 1918, soon after the first frosts, had an elaborate reddish color pattern over the entire body, and the wings were a decided brown. This discol-

oration was brought on gradually during the fall of 1918 in specimens of *C. rufilabris* and *C. quadripunctata* which were placed in outdoor cages and fed on a weak sugar solution. As the cold weather came on, the discoloration became gradually more pronounced. Discolored adults of *C. plorabunda* are very common in Kansas in the fall and spring. The reddening appears with the first cold weather in the fall and persists until the adults begin to take food in the spring. Some specimens retain a little of the green, but the majority lose most of the normal coloration. Both males and females overwinter and thus become discolored.

It has been found that at any time during the winter the discolored adults of *C. plorabunda* may be brought into the laboratory and the normal green color restored. It appears that food is more important than temperature in this restoration, though this species has not been observed to take any food in confinement other than water, weak sugar solution, plant sap, and, less commonly, crushed aphids. The coloration has been restored in from one to two weeks by feeding water alone, or sugar solution, while the insects were confined in the laboratory.

FIRST APPEARANCE OF THE ADULTS IN THE SPRING

The time of the first appearance in the spring varies with the manner of overwintering and the climate. Adults of *Chrysopa plorabunda* have been taken throughout the winter in Kansas. At Charlottesville, Virginia, the first adult of *C. oculata* was seen on March 20, 1919; at Ithaca the first adult was seen the first week in May, 1916, but it is doubtful whether this was among the first to emerge. Adults of *C. quadripunctata* and *C. nigricornis* were taken the latter part of May, 1921, in Kansas, and in June, 1917, at Ithaca and in Kansas. It has been observed for four years that June is the earliest date when a variety of Chrysopidae has been taken by collecting. Adults were obtained during all the winter and spring months by bringing overwintering cocoons indoors, into a room of fairly constant temperature. Some individuals pupated promptly, while others made apparently no change for a month or more. Some prepupae died when brought indoors in the course of these studies, but pupae very rarely died in cocoons.

FACTORS REDUCING THE NUMBER OF INDIVIDUALS

Several papers dealing with the parasites of the Chrysopidae have been published. Howard (1888), Girault (1907 b), and McGregor (1917) have given lists of parasites. Moffat (1901) discusses egg parasitism but lists no species. So far three egg parasites, one larval parasite,

sixteen primary pupal parasites, eight secondary pupal parasites, and one adult parasite, have been recorded for the Chrysopidae. The predacious enemies recorded are certain birds (Wildermuth, 1916), and a larva of *Anatis 15-punctata* (Schwartz, 1890).

Parasites

Egg parasites

Trichogramma minutum Riley was the only egg parasite reared during these studies. This parasite attacks the eggs of a large number of different insects, but, so far as is known, has not before been reported as attacking eggs of the Chrysopidae. Its life history has been given by Bodkin[3], together with valuable biological notes on the species. Parasitized eggs turned to a smoky color in about three days, and jet black with a peculiar dull appearance in another day. One egg was glued fast to a leaf by a gelatinous substance, but later examples show this to have been an exception. When mature the adult parasite emerged through an irregularly circular hole eaten in the side of the egg. This parasite is of no appreciable importance inasmuch as its occurrence in nature is rare. Its life history may be readily studied by obtaining the parasites from some other host—as, for example, eggs of the corn-ear worm (*Chlorida obsoleta* Fab.)—and inducing parasitism on chrysopid eggs.

Larval parasites

Only one parasite attacking the larva was taken. This was a parasitic chigger mite of the genus Erythraeus (Hartzel, 1918). While the writer was collecting on the grounds of the Soldiers' Home at Milwaukee on August 25, 1917, a number of larvae of *Chrysopa rufilabris* were taken which had one or more of these bright red mites attached. They remained attached to the larvae for several days when the larvae were confined in vials, and a few remained permanently attached when the larvae were preserved in alchohol. Larvae thus parasitized showed very slow growth.

Pupal parasites

Considering the word *pupa* here as including the prepupa, which stage is also spent inside the cocoon, a number of important pupal parasites have been obtained. The primary and secondary parasites that have emerged from cocoons are given in the accompanying table.

[3]Bodkin, G. The egg parasite of the small sugar cane borer. Board Agr. British Guiana. Journ. 6:188-198. 1903.

Parasite	Host species	Locality	Date	Determined by
Helorus chrysopae	*Chrysopa oculata* (?)	Ithaca	August 25, 1916	Dr. J. C. Bradley
Perilampus sp.	*C. oculata* (?)	Ithaca	August 22, 1916	Professor C. R. Crosby
Hemiteles areator subsp. *tenellus*	*C. nigricornis*	Ithaca	October 20, 1916	Dr. J. C. Bradley
Hemiteles tenellus Say	*C. rufilabris*	Charlottesville	August 11, 1918	A. B. Gahan
Perilampus chrysopae Cwfd.	*C. rufilabris*	Charlottesville	August 11, 1918	A. B. Gahan
Tetrastichus chrysopae Cwfd.	*C. rufilabris* (secondary)	Charlottesville	August 11, 1918	A. B. Gahan
Arachnophaga sp.	*C. lateralis*	Florida	September 4, 1918	A. B. Gahan
Parataneostigma nigriaxillae Gir.	*C. lateralis*	Florida	September 9, 1918	A. B. Gahan
Isodromus atriventris Ash.	*C. lateralis*	Florida	August 24, 1918	A. B. Gahan
Horismenus sp.	*C. lateralis*	Florida	September 12, 1918	A. B. Gahan
Dibrachys bouchearus Ratz.	*C. rufilabris* (secondary)	Milwaukee	August 25, 1917	A. B. Gahan
Perilampus chrysopae Cwfd.	*C. rufilabris*	Dayton, Ohio	August 26, 1921	A. B. Gahan
Tetrastichus (Geniocerus) chrysopae Cwfd.	*C. rufilabris*	Dayton, Ohio	August 26, 1921	A. B. Gahan

The information obtained concerning the life histories of these parasites and hyperparasites is fragmentary. Parasitized cocoons in all cases gradually turn dark to decidedly black. When parasites have emerged, one can usually find the shriveled skin of the prepupa in the

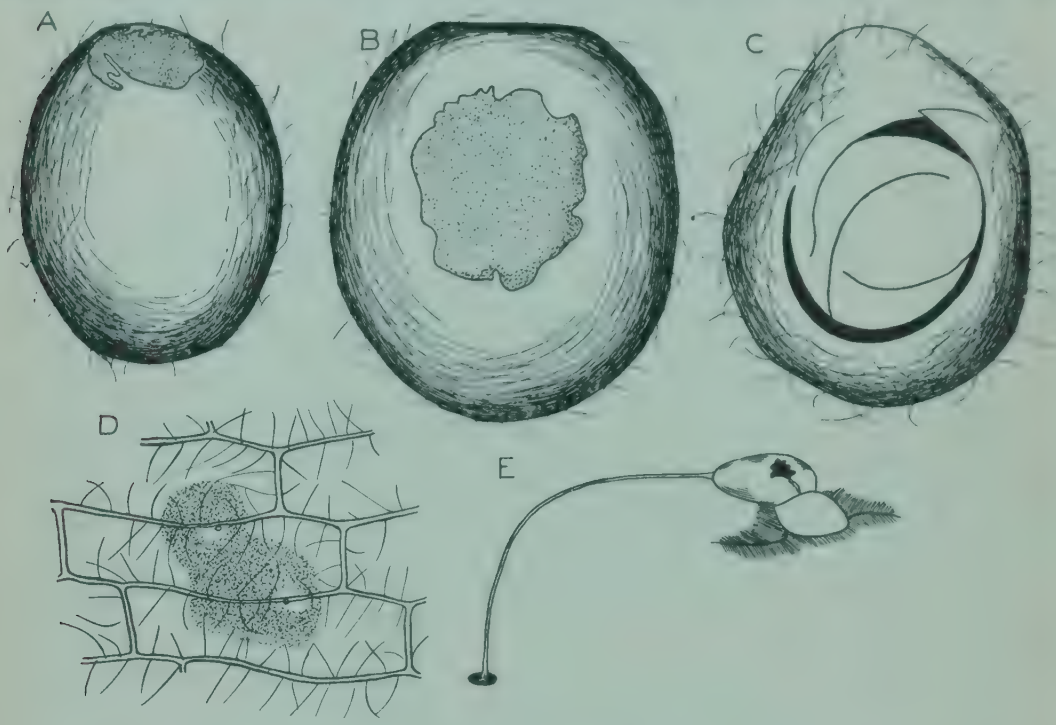


FIG. 160. WORK OF PARASITES ON CHRYSOPIDS

A, Empty cocoon of Chrysopa rufilabris from which Hemiteles areator subsp. tenellus emerged, x 11¾

B, Cocoon of C. oculata from which Perilampus sp. emerged, x 11¾

C, Cocoon of C. oculata from which Helorus chrysopae emerged, x 11¾

D, A piece of a wing of C. oculata showing two feeding punctures of Pseudoculicoides eques and the brownish area around each

E, Egg of C. oculata from which Trichogramma minutum emerged, showing the clear gelatinous substance holding the egg to the leaf, x 11¾

case, together with the thin, filmy cocoon of the parasite. In all cases so far seen, the parasite destroys the chrysopid prepupa before it pupates. The parasites make several kinds of openings in the cocoons at emergence, that of *Helorus chrysopae* being especially interesting (fig. 160, C).

In general, the pupal parasites are the greatest check on the Chrysopidae. Parasitized cocoons of *Chrysopa rufilabris*, *C. nigricornis*, and others occurring in the open, were frequently collected. McGregor

(1914), and McGregor and McDonough (1917), reported a parasitism of 55.9 per cent. There was never a parasitism even approaching this figure noted during these observations.

Parasites of the adult

Pseudoculicoides eques Johannsen (Plate LXXXVIII) was found to be fairly common on the wings of several species of Chrysopidae. This is a little blood-sucking chironomid, which sits on the wings, buries its proboscis in a vein, and sucks up the blood of its host. At Ithaca during the month of July, 1916, an average of 9.5 per cent of all the *Chrysopa oculata* adults collected had one or more of these parasites on their wings. They were taken on the wings of *C. oculata* and all its varieties, *C. chi* and its variety, *C. nigricornis,* and *Meleoma signoretti.* The parasites appear to have no choice as to the veins of their host, and as many as three may be found on one wing. They sit motionless while on the wings and hold on firmly even while the host is flying. The abdomen is generally distended. When disturbed the parasites fly very rapidly, practically leaping from place to place. Only females were found on the wings. The life history is unknown. The species was observed only in New York State.

The parasitic mite Erythraeus also attacks the adult chrysopids. The mite remains securely attached to the body of its host. Specimens of *C. rufilabris* thus parasitized were taken on goldenrod in the woods, at Milwaukee.

Predacious enemies

Wildermuth (1916) points out that certain birds, such as the western wood pewee and the nighthawk, feed on adult Chrysopas in spite of their repellent odor. He states also that robber flies have been noted as catching the adults, and that some Hemiptera prey on the larvae. The writer has given live adults to a praying mantis, which devoured several daily. A red-headed woodpecker was seen to catch an adult, probably *Chrysopa nigricornis,* on the wing and devour it. It was observed that coccinellid larvae would eat eggs of *C. oculata* but did not devour larvae of the same species.

FACTORS AFFECTING THE SPREAD OF THE SPECIES

Most of the species of Chrysopidae studied have a wide distribution. Their flight is not adapted to long distances. It seems probable that the gradually increasing range of the species is being brought about

through the shipping of hay, grass, logs, trees, shrubbery, and the like. Cocoons occur on various parts of these and may readily be shipped even to considerable distances. Professor C. R. Crosby found fourteen chrysopid eggs on the window of a moving train, and this suggests a ready means of spread. Adults may enter open box cars during the day and be transported to a considerable distance.

ECONOMIC IMPORTANCE OF THE FAMILY

Both larvae and adults of all our species of Chrysopidae are distinctly beneficial. The only instance on record of this family's doing any harm was in California, where the larvae were reported by Essig (1911) as destroying the larvae of ladybird beetles which had been introduced to combat scale insects. During the course of these rearings several species of coccinellid beetles were successfully reared in the same vials with chrysopids, but there were usually some aphids present.

Chrysopid larvae are occasionally an annoyance to man by their biting, which suggests a pin prick, and by their crawling over his person. This occurs most frequently under trees or in fairly dense vegetation. The tree and shrub chrysopid species are most commonly the source of this annoyance, but any hungry, grown, third-instar larva appears to be capable of piercing the skin and sucking some blood if not disturbed (Marchand, 1922).

The chief contribution of the Chrysopidae to human welfare is their destruction of plant lice during the summer and autumn months. They do not appear early enough in the year, nor are they present in sufficient numbers, to appreciably check fruit injury by plant lice or to reduce early spring outbreaks of aphids such as that of the pea aphids on alfalfa in Kansas early in 1921. But as summer progresses, the tree-inhabiting species become sufficiently numerous to take an important part in combating the woolly apple aphis on elm, the painted maple aphis, the maple Phenococcus, the apple leaf hopper, and similar pests. Aphids attacking cereal and forage crops are preyed upon by *Chrysopa oculata*, *C. plorabunda*, and *C. rufilabris*, chiefly. These species are usually present in clover and alfalfa fields, sorghum fields, and cornfields, sometimes in great numbers. While it is the larvae that are generally seen devouring the plant lice in the field, nevertheless there is no doubt that the adults of our common species regularly prey upon plant lice, with the possible exception of *C. plorabunda*, and thereby increase the importance of this family economically.

One is likely to give the Coccinellidae and the Syrphidae some of the credit for aphid destruction which is really due to the Chrysopidae.

for, on examination of an aphid-infested plant, these insects are usually first seen, the chrysopids being more difficult to find.

The parasitic Hymenoptera and the Coccinellidae are generally more plentiful and more effective checks upon aphids than the chrysopids, though this varies with the locality and other conditions. In one field where the melon aphis was plentiful, these enemies were very scarce while *Chrysopa oculata* was exceedingly abundant.

DESCRIPTIONS OF THE LIFE STAGES OF THE SPECIES

It will be soon observed that the chief points emphasized in the following descriptions are color patterns. The reader is cautioned against too strict interpretation of color shades and of sizes and shapes of spots, for both are subject to variation. However, the variation does not extend to such lengths as to make the species difficult to recognize, with the possible exception of the *rufilabris-plorabunda group*. With a little practice, all the larvae described may be recognized at a glance in the third instar. The other instars are more difficult of recognition because of size and less distinct coloration.

Chrysopa oculata Say (Plate LXXIX)

1839 *Chrysopa oculata.* Say, Journ. Acad. Nat. Sci. Phila., vol. 8, p. 9-46.
1839 *Chrysopa chlorophana.* Burmeister, Handbuch Ent., vol. 2, p. 979.
1855 *Chrysopa albicornis.* Fitch, First report, p. 84.
1903 *Chrysopa chlorophana.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 147.
1903 *Chrysopa albicornis.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 149.
1903 *Chrysopa oculata.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 152.

Chrysopa albicornis Fitch is placed under *C. oculata* Say for the following reasons:

1. There is no definite boundary between the two forms, the only differences being in their size and in the degree of darkening of the wings. A series may be readily arranged from one to the other.

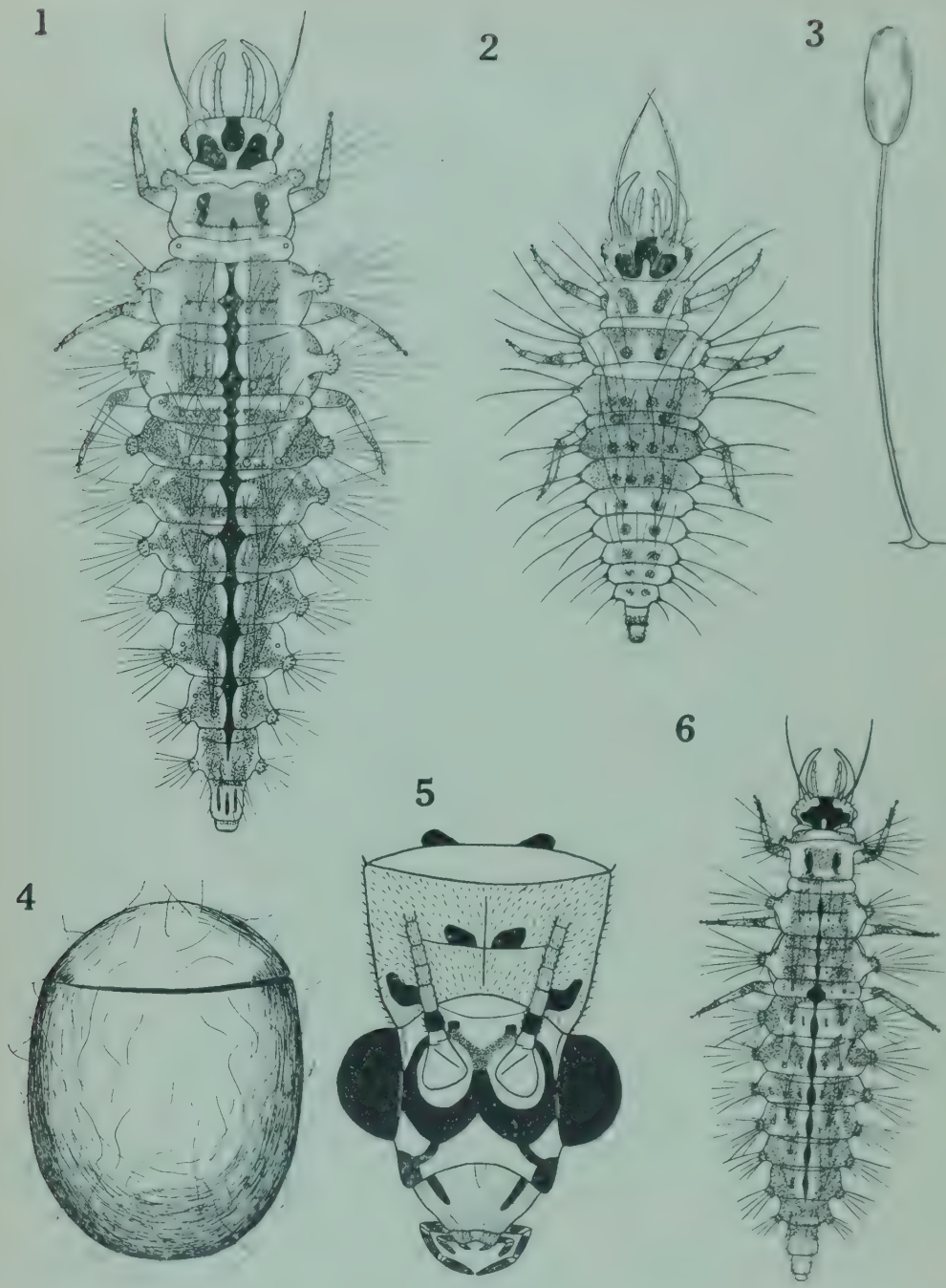
2. The great majority of specimens answering the description of the former are males. It has been found that the males show a tendency to be smaller and darker than the females.

3. The progeny of several females answering the description of *albicornis* gave all medium-dark-winged to light-winged specimens *(oculata).*

4. The dark specimens cross readily with any variety of *C. oculata.*

5. The dark specimens occur with *C. oculata* in nature in the same habitats and have no distinguishing habits.

6. The eggs and the larvae of the two forms are indistinguishable.



CHRYSOPA OCULATA

1, Mature third-instar larva, x about 10¾. 2, Newly hatched first-instar larva, x about 18; dotted part of abdomen showing coloration due to first meal. 3, Egg, x about 10¾. 4, Cocoon, showing lid, x about 10¾. 5, Head and prothorax of adult, showing color pattern, x about 10¾. 6, Second-instar larva, x about 10¾

C. chlorophana Burm. is included under *C. oculata* Say for the following reasons:

1. The progeny of wholly-green-winged females have nearly always been *oculata*. Very few forms with wings of a permanently pure green have yet been obtained in rearings from any variety of *oculata*.

2. The great majority of individuals of this variety have been found to be females. Males are scarce. Females of *C. oculata* of the dark medium type tend to be larger and have lighter wings, and so a series can be arranged from the darkest to the wholly-green-winged varieties.

3. *C. chlorophana* crosses readily with any variety of *C. oculata*, including *albicornis*.

4. It occurs in nature with *C. oculata* and can be taken in the same habitat.

5. The life history stages of the two forms are indistinguishable.

The average length of time for the various stages of the life history of ten individuals of *Chrysopa oculata* reared in the laboratory in the early spring of 1916 was, respectively: egg stage, 5.4 days; first instar, 7.3 days; second instar, 3.9 days; third instar to spinning of cocoon, 3.9 days; within the cocoon, 26 days.

This is by far our most abundant species. The writer has collected specimens in New York, Ohio, Virginia, Wisconsin, and Kansas. The species is a member of the field group, and in general collecting in the East it always predominates. It has the greatest range of any of our species. Descriptions of the stages from the medium-dark-type parentage only are here given, as the types are all identical.

Egg.—Elongate-elliptical, light bluish or yellowish in color, normally on a long, hyaline stalk. Chorion smooth, unmarked. Micropyle button-like, white, rarely with a tinge of green. Length of egg, 1.03 to 1.1 mm.; diameter, 0.42 to 0.49 mm.; length of stalk, 3.4 to 4.8 mm.

First-instar larva (just hatched).—A large black spot on dorsum of head, deeply notched behind. Body gray to flesh-colored. Two setae from prothoracic tubercles; three from each mesothoracic and metathoracic tubercle; two each, an upper large one and a lower small one, from abdominal tubercles 2 to 7; dorsal tubercles on thorax prominent, each bearing a single seta; an outer pair of dorsal tubercles and an inner pair of papillae on each of abdominal segments 1 to 6, each bearing a single seta. Dark spots around base of each of the abdominal dorsal papillae and tubercles. Total length of larva, 1.88 mm.; length of head, 0.54 mm.; length of mandibles, 0.39 mm.; width of head, 0.33 mm.; width at metathorax, 0.38 mm.; length of longest setae on body, 0.47 mm.

Second-instar larva.—Head with same coloration as in previous instar; antennae, jaws, and palpi yellowish to brownish in color; prothoracic tubercles prominent, dark in color; a patch of light brown or reddish brown on anterior side of stalk. About ten long and short setae from each tubercle. Mesothorax

and metathorax very similar; first subsegment of mesothorax entirely grayish, less commonly with slight reddish areas on each side of dorsal vessel; first subsegment of metathorax very small, entirely gray except a small white spot on each side of dorsal vessel; second subsegment of each of similar color pattern; tubercles entirely white to light grayish; on each side of dorsal vessel a white area. First segment of abdomen rounded at sides, not bearing tubercles; lateral tubercles on second segment prominent, dark brownish black; on segments 3 to 7 inclusive, lateral tubercles white, with a small, reddish brown, elongate spot on upper side of each stalk; setae and their bases black; outer dorsal tubercles bearing two setae each, the inner pair one each; just in front of outer pair of dorsal tubercles, a prominent reddish brown to flesh-colored spot. Total length from tail to tips of mandibles, 4.8 mm.; width at metathorax, 1.3 mm.; length of mandibles, 0.53 mm.; width of head, 0.6 mm.; length of head, 0.3 mm.

Third-instar larva.—General coloration and form very similar to that of second instar. Dorsal head pattern distinctive of instar. Head grayish, with three large, distinct, black spots on dorsum; mandibles amber-colored; antennae dark. Legs dark near joints. First subsegment of prothorax having grayish area in median line; base of first pair of tubercles reddish brown; second and third lateral tubercles yellowish, bearing fifteen to twenty setae each; a large reddish brown patch near base of stalk on anterior side of each; an irregular reddish brown area on each segment from base of stalks to yellow border of dorsal vessel. First pair of lateral abdominal tubercles lacking; second pair brownish black, specific; other tubercles reddish brown, but with their bases yellow, forming an irregular yellow border for the abdomen on each side; reddish brown area extending forward in front of each abdominal tubercle, reaching yellow border of vessel; a yellow area reaching this reddish area just in front of it. Eighth abdominal segment yellowish in center, borders pale; ninth segment with brown area in front; tenth segment nearly wholly brown. Length, 9 mm.; width at metathorax, 2 mm.

Pupa.—(The larva usually spins a pure white silken cocoon, but it may fail to do this.) Appearance of cocoon papery, with straggling threads issuing. Length of cocoon, 3.4 to 3.6 mm.; width, 2.7 to 2.9 mm. (For characters of pupa, see head characters of adult).

Adult.—Face pale yellowish; two broad loops of shining black under both antennae; median prong of color ending between antennae; a prominent loop of black near each eye, joining sub-antennal loops; a red or reddish yellow triangle above, with four occipital dots above this, these dots often connected; occiput distinctly yellow; basal joint of antennae and antennal areas of head gray to yellowish; second joint of antennae with black ring; remainder of antennae very light brown; clypeus reddish, with black dots at sides; labrum reddish; palpi broadly banded with black. Two prominent black spots at outer anterior margins of prothorax; eight small black dots on dorsum of prothorax behind these, often indistinct. Thorax and abdomen light green, generally unmarked except by darkened areas of viscera. Wings hyaline, varying from having all veins and veinlets green to a considerable degree of darkening; tips rounded. Length from head to tips of wings, 15 to 20 mm.

Chrysopa nigricornis Burmeister (Plate LXXX)

1839 *Chrysopa nigricornis.* Burmeister, Handbuch Ent., vol. 2, p. 979.
1861 *Chrysopa nigricornis.* Hagen, Synopsis Neuroptera N. Amer., p. 214.
1903 *Chrysopa nigricornis.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 149.

Chrysopa nigricornis is one of our largest species. Adults can be taken at lights from June to September. This is a tree and shrub species. Larvae have been repeatedly taken on maple trees in late summer, when the painted maple aphis is most abundant. The species has also been taken repeatedly on oak, elm, tulip tree, spiraea, and red osier (dogwood). Specimens have been collected at Ithaca, Milwaukee, Dayton, Charlottesville, and Manhattan (Kansas).

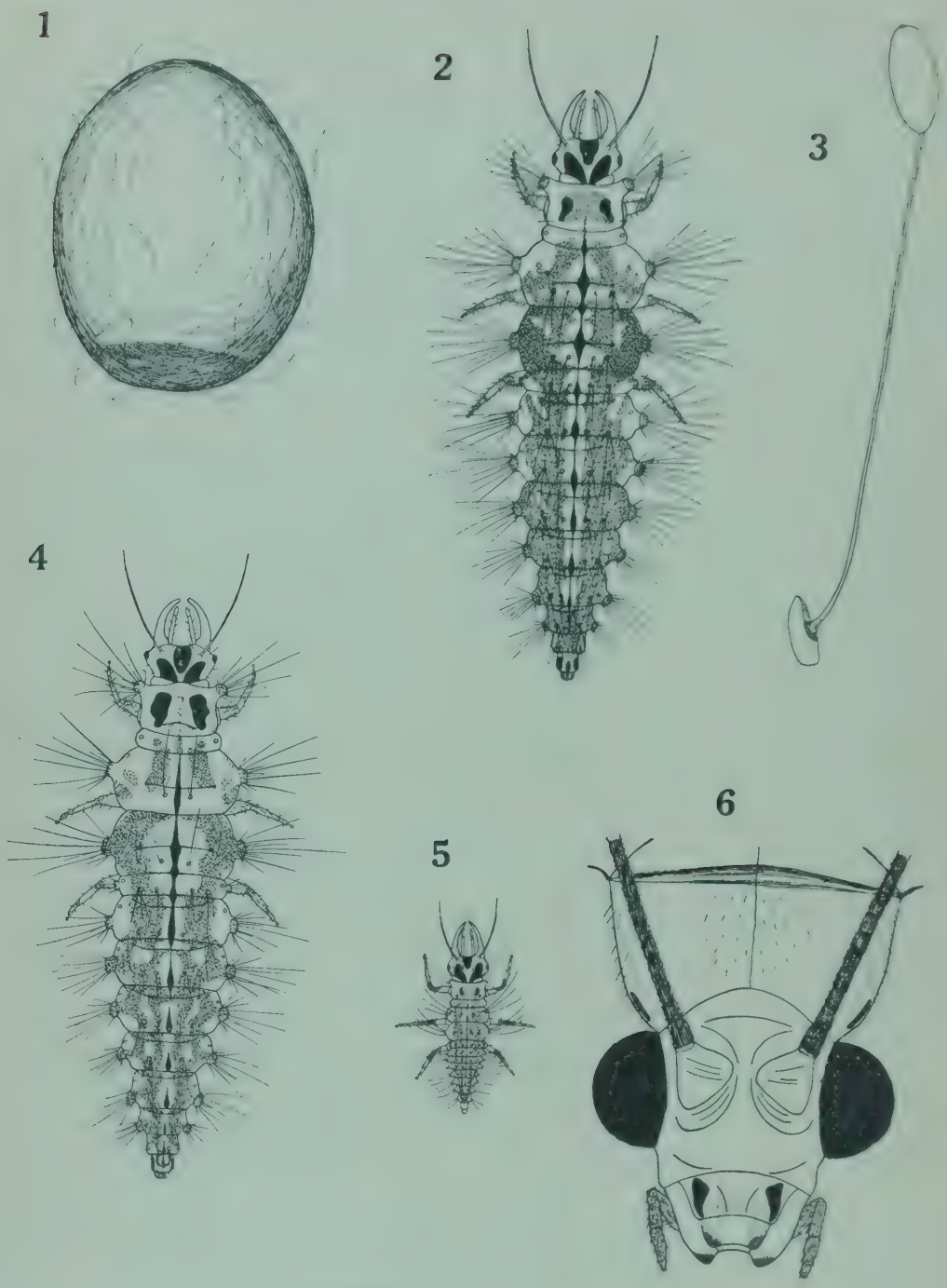
The life history of some of the specimens observed may be summarized as follows:

Number of specimen	Date egg was laid	Date of hatching	Date of first molt	Date of second molt	Date cocoon was spun	Date adult emerged
54.1	Sept. 2	Sept. 7	Sept. 11	Sept. 16	Sept. 28	Wintered
54.3	Sept. 2	Sept. 7	Sept. 11	Sept. 17	Sept. 28	Wintered
54.2	May 22	May 27	June 6	June 9	June 12	June 25
56.4	Dec. 9	Dec. 16	Dec. 21	Dec. 24	Dec. 29	Jan. 9
67.5	May 22	May 28	June 6	June 9	June 12	June 28

Egg.—Elongate elliptical, light green with yellowish tinge, becoming more yellow as embryo develops. Eggs laid singly or in close groups. Length of egg, 1.02 to 1.09 mm.; width at middle, 0.38 to 0.42 mm.; length of stalk, 7.5 to 8.6 mm.

First-instar larva.—Head grayish or yellowish, large with three spots above. Thorax grayish to dark; whitish area on each side of dorsal blood vessel throughout its length. Two setae from prothoracic and all lateral abdominal tubercles; three setae each from meso- and metathoracic lateral tubercles. First two pairs of thoracic tubercles grayish to yellowish; third pair black or reddish; first pairs of lateral abdominal tubercles white, fairly well developed. Medial setae prominent. A dark spot at base of each dorsal abdominal tubercle. Length of newly hatched larva, 1.5 mm.; width of head, 0.32 mm.; width at metathorax, 0.32 mm.; length of lateral setae, 0.29 mm.

Second-instar larva.—Three separate spots on dorsum of head. First two pairs of lateral tubercles grayish; third pair dark brown to blackish brown. First abdominal segment bearing a pair of small lateral tubercles beset with about five short, white setae. Dorsum of abdomen dark; border of gray on each side of vessel; near end of instar, reddish spots appearing in this gray border. First two abdominal tubercles white to gray; others dark to brownish black; tubercles bearing six to ten setae each, two large, the remainder smaller. Early second-instar larvae rather dark; late second-instar larvae reddish brown, much like *C. oculata*; color pattern tending to break up into irregular reddish brown patches. Legs wholly gray; distal ends of tibiae and tarsi black. Width of head, 0.57 mm.; length of mandibles, 0.49 mm.; length of antennae, 0.8 mm.; total length of larva, 5.95 mm.; length of setae, 0.46 mm.



CHRYSOPA NIGRICORNIS

1, Cocoon, showing black disk of last larval molt. 2, Mature second-instar larva. 3, Normal egg. 4, Early third-instar larva. 5, First-instar larva, just hatched. 6, Head of adult, the two-spotted type

(All x about 10¾)

Third-instar larva.—Head gray or yellowish; three separate black spots above; mandibles, palpi, and antennae light amber, tips of mandibles darker. First subsegment of thorax gray, darker at sides; second subsegment largely dark brown to brownish black, border smoky gray, reddish below; reddish between prothoracic depressions. First subsegment of mesothorax gray, crossed by reddish areas; second subsegment reddish black except grayish borders and a small gray area on each side of dorsal vessel; in these gray areas some bright red spots. Prothoracic and mesothoracic tubercles similar, bearing twelve to eighteen setae; bases of all black; apical setae larger than basal ones. Metathorax black or brownish black except a prominent gray area on each side of vessel, with bright red spots in same. First abdominal tubercle well developed, pure white, bearing white setae; second pair of tubercles also white, with a tinge of red on stalks; remainder of tubercles alike, grayish variously marked with dark red, bearing twelve to fifteen setae, three to five large black ones and the remainder smaller and white; from border to gray area along vessel, black, almost uninterrupted in early third-instar larvae, later breaking up into poorly defined reddish black blotches. Width of head, 0.92 mm.; length of mandibles, 0.8 mm.; total length of larva, 9.1 mm.; width at metathorax, 3 mm.; length of abdominal setae, 0.7 mm.

Pupa.—Pupal stage generally passed in a silken cocoon. Cocoon elongate spherical, pure white, appearing like paper but with few free threads; opening by lid at upper end. Length of cocoon, 4.1 mm.; width, 3.3 mm. (For late pupae, the head characters of the adult are useful in identification.)

Adult.—Head grayish green, darker above; usually two elongate marks on outer margins of clypeus (in some cases two more black dots on genae); clypeus with row of setae; labrum distinct, bordered with setae; area about basal antennal joint depressed, first joint grayish green, from the second to the end of about the basal fifth jet black to brownish, fading into light brown which persists to tip. Prothorax wholly green, usually with two black spots at outer anterior margins; two or three small median black dots seen in some specimens, otherwise entire thorax and abdomen light green. Wings long, acute at tips, rather narrow; pterostigma prominent; gradate veinlets and others dark. Length of adult, 15 to 20 mm.

Chrysopa quadripunctata Burmeister (Plate LXXXI)

1839 *Chrysopa quadripunctata.* Burmeister, Handbuch Ent., vol. 2, p. 980.
1851 *Chrysopa quadripunctata.* Schneider, Symb. ad monograph. gen. Chrysopae, p. 84.
1861 *Chrysopa quadripunctata.* Hagen, Synopsis Neuroptera N. Amer., p. 218.
1903 *Chrysopa quadripunctata.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 153.

The species *Chrysopa quadripunctata* also is arboreal. It was taken most frequently in a dense thicket of oak and underbrush at Charlottesville; at lights and by sweeping goldenrod in shaded localities, preferably near oaks and on maple and spiraea, with *C. nigricornis*, at Ithaca and Milwaukee; in dense woods on goldenrod at Dayton; on elm, maple, and apple at Manhattan. This is a very beautiful species and is quite distinct. In habits it is much like *C. nigricornis*, except that the larvae are very frequently seen with some trash on their backs.

The life history as observed in some specimens may be summarized as follows:

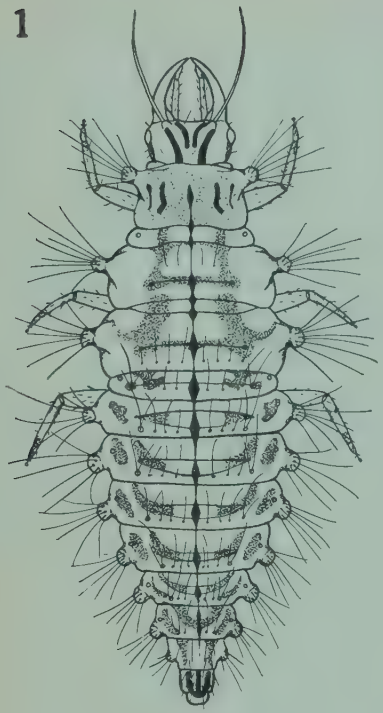
Number of specimen	Date egg was laid	Date of hatching	Date of first molt	Date of second molt	Date cocoon was spun	Date adult emerged
71	Sept. 9	Sept. 15	Sept. 19	Sept. 24	Oct. 8	Wintered
72	Sept. 7	Sept. 11	Sept. 15	Sept. 20	Sept. 28	Wintered
73	Sept. 6	Sept. 10	Sept. 14	Sept. 18	Oct. 3	Wintered

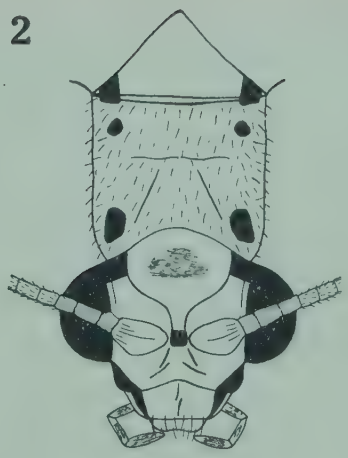
Egg.—Stalked, laid singly; oftenest found on trees (especially maple) and shrubs. Smaller than most chrysopid eggs, very light green to yellowish green. Chorion unsculptured. Length of eggs, 0.84 mm.; width, 0.38 mm.; length of stalk, 4.4 to 4.6 mm.

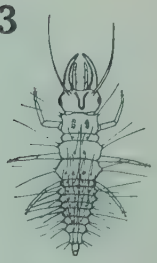
First-instar larva.—Very pale, somewhat translucent. Contractions of pharynx observable as larva feeds, appearing as an hourglass-shaped structure in dorsal view, slightly darkened; later four narrow bands on dorsum of head, converging behind. Body unmarked except anterior of abdomen, which is darker, due to food. Lateral tubercles prominent; setae long and stout, two on each prothoracic tubercle, three on each meso- and metathoracic lateral tubercle. No setae on first abdominal segment, which is also without tubercles; on each of lateral tubercles 2 to 7 inclusive, two setae, a large upper and a small lower one; two pairs of dorsal papillae on each abdominal segment from first to sixth inclusive; on thorax and beyond sixth segment, but one pair each.

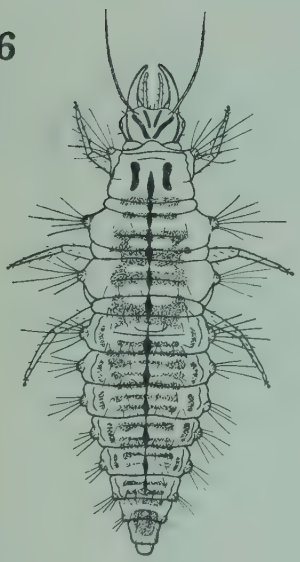
Second-instar larva.—General color gray, with brown to brownish black markings. Head entirely gray above; two pairs of converging black marks at midline; two narrow bands extending posteriorly from outer margin of antennae and converging; two others between these, shorter, converging behind. First subsegment of prothorax grayish white, both above and on sides. Thoracic tubercles large and prominent, wholly light grayish in color; setae medium long, eight to ten on each tubercle; paired dark brownish to black markings on thorax at each suture; black of dorsal vessel widening out at each suture, between these large patches of color and the sides, smaller areas of reddish brown. Fifth, sixth, and seventh abdominal segments with a little of this reddish brown mixed in the large spots; eighth abdominal segment with a large central black spot; ninth with a basal black spot; tenth slightly yellowish brown, without dark spots; segments 2, 3, 4, and 5 showing brownish spots on sides beneath lateral tubercles; a few dorsal setae, small and inconspicuous, most prominent on segments 5, 6, 7, and 8.

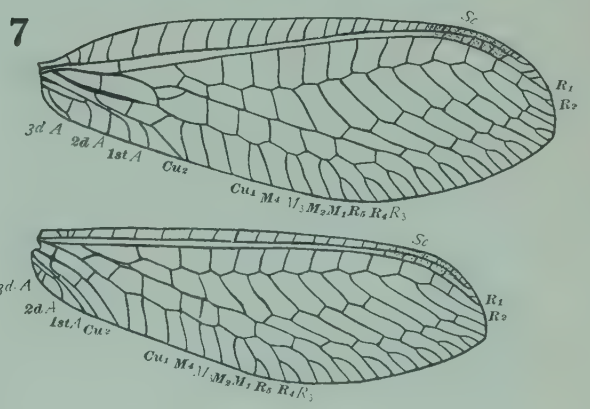
Third-instar larva.—General color gray, marked with brown to brownish black. Head grayish, four converging narrow brown bands above; middle pair of bands short, curved toward each other abruptly, and extending posteriorly to middle of head; outer pair narrow in front, broadening out in posterior half, extending from bases of antennae to first subsegment. Lateral tubercles of thorax and abdomen wholly gray. Two patches of brownish extending from prothoracic depression to metathorax, these increasing in width until they are broadest at metathorax, so that this is the darkest part of the body. Prominent gray bordering each side of dorsal vessel. Thoracic markings extending back over abdomen to fourth abdominal segment, decreasing in intensity and disappearing at fourth segment; from fourth to seventh segment, abdomen mostly











CHRYSOPA QUADRIPUNCTATA

1, Third-instar larva, about midway in the instar. 2, Head and prothorax of adult, showing markings. 3, Newly hatched larva. 4, Normal egg. 5, Cocoon. 6, Second-instar larva. 7, Right wings of adult
(All x about 10¾)

gray; first abdominal segment with no prominent lateral tubercles but some short setae on sides; some variation in coloration, chiefly in the amount of brown. (This larva was nearly ready to pupate; less advanced ones are darker.)

Pupa.—Cocoon slightly elongate spherical, of dense, pure white silk. Length of cocoon, 3.4 mm.; width, 2.6 mm. Late pupa with markings of adult faintly outlined. Early pupae difficult to classify.

Adult.—Head yellow above, gray below; antennae with a prominent reddish brown or maroon stripe from eyes to mouth; an orange spot between bases of antennae; a pair of elongate orange spots above eye; occiput pure yellow; distal segment of palpi brownish; antennae wholly pale. Body bluish green, with a fairly prominent yellowish dorsal area. Prothorax marked above with two pairs of orange spots. Mesothorax with a pair of orange spots in front. Abdomen yellowish above, green on sides; first three segments variously marked with orange on sides. Wings fairly broad; front pair scarcely acute at tips; hind pair acute at tips; gradate veinlets brownish black; ends of costals and radial sectors brown; pterostigma distinct. Length of adult, 12 to 16 mm.

(There is some variation in the size and intensity of the color spots. The orange spots vary to reddish and the yellow dorsal area varies in prominence. There is also some variation in the length of the adults.)

Chrysopa chi Fitch (Plate LXXXII)

1855 *Chrysopa chi.* Fitch, First report, p. 87.
1855 *Chrysopa upsilon.* Fitch, First report, p. 87.
1861 *Chrysopa chi.* Hagen, Synopsis Neuroptera N. Amer., p. 213.
1861 *Chrysopa ypsilon.* Hagen, Synopsis Neuroptera N. Amer., p. 213.
1903 *Chrysopa chi.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 148.
1903 *Chrysopa ypsilon.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 148.

The two species *Chrysopa chi* and *C. upsilon* are described by Fitch and designated the *X* and *Y spotted golden eyes.* Hagen (1861) redescribed both species, and after his description of *C. "ypsilon"* he added: "At first sight it resembles the preceding [*C. chi*]; is it different?" Banks (1903) describes the two species in comparison, and adds: "It [*C. "ypsilon"*] is very close to *Ch. chi*, but the difference in head-markings appears to be constant."

The writer has carefully reared both the *X* and the *Y* variety, and has concluded that they are the same species for the following reasons:

1. Batches of eggs from either variety yielded adults marked the same as the other, as well as intermediate varieties.
2. The larval colorations were identical.
3. The adults of both varieties occurred in the same habitats.
4. There was an intergradation of the head markings. Six steps in this intergradation are shown in Plate LXXXII, 7, and others may be added though they are less distinctive. To illustrate the proportion of each of these steps, the catch from a trip on June 22, 1916, was classified. These specimens were all taken within an area of an acre. Of the 87

specimens, 20 were No. 1, or true *C. chi*, 17 were of the second variety, 10 were of the third, 15 were of the fourth, 11 were of the fifth, and 14 were of the sixth, or true *upsilon*, variety.

Both of these species were described by Fitch at the same time, and on the same page of his report. *C. chi* was the first described, and therefore becomes the true species, and *C. upsilon* becomes a synonym. It appears from rearings and collections that *C. chi* is slightly more abundant than *C. upsilon*. It is an early species, having been found fairly abundant at the McLean bogs in the middle of June, in goldenrod patches. It has been taken also in Ithaca, along shaded hedges and on spiraea, in June.

The life history of some specimens of *C. chi* may be summarized as follows:

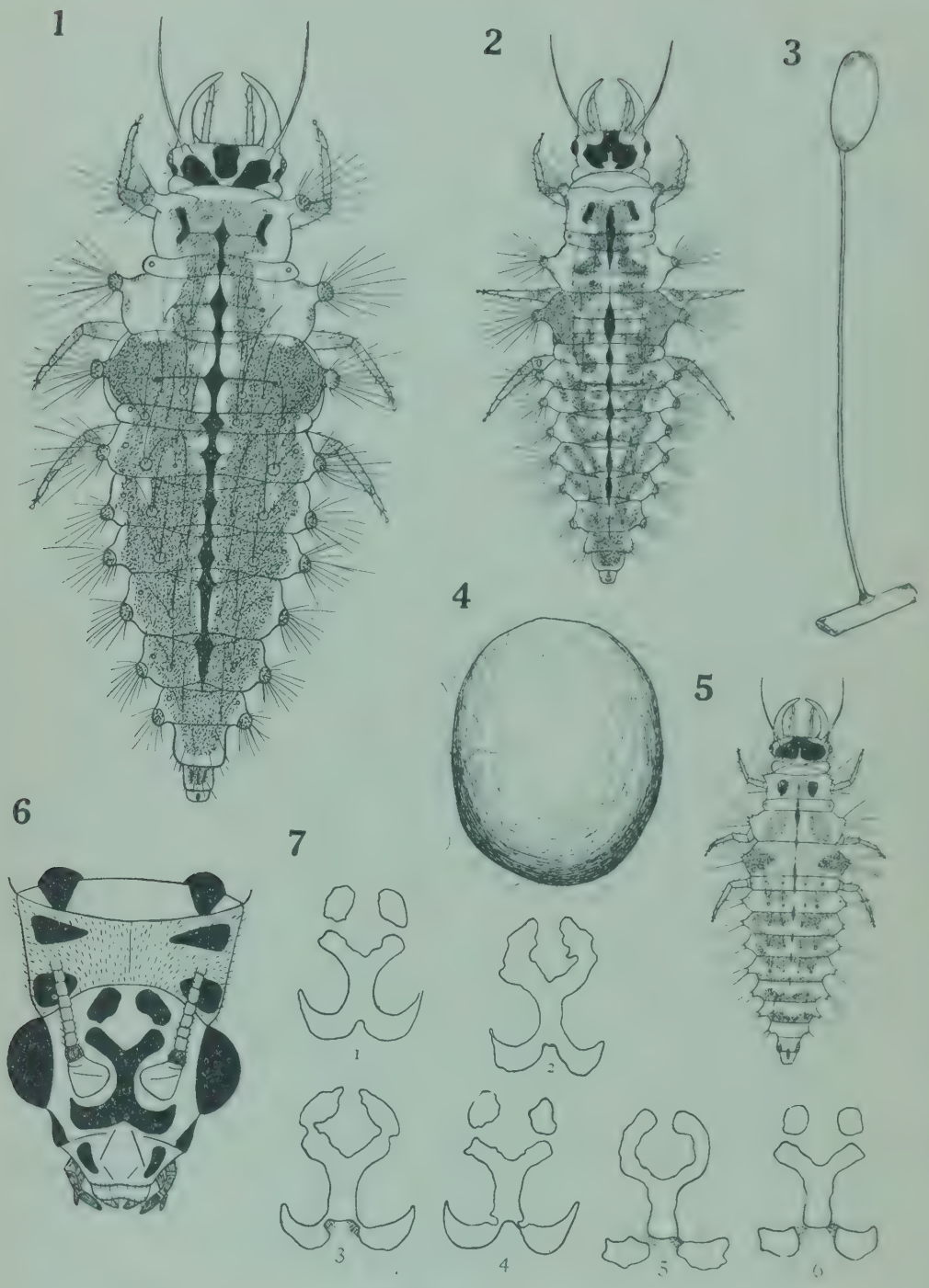
Number of specimen	Date egg was laid	Date of hatching	Date of first molt	Date of second molt	Date cocoon was spun
57.1	July 15	July 20	July 23	July 26	Aug. 2
57.2	July 15	July 20	July 23	July 26	July 30
57.3	July 15	July 20	July 24	July 26	Aug. 1

The life history of some specimens of the *upsilon* variety was as follows:

Number of specimen	Date egg was laid	Date of hatching	Date of first molt	Date of second molt	Date cocoon was spun	Date adult emerged
60.1	July 15	July 20	July 24	July 27	Aug. 1	Aug. 15
60.2	July 15	July 20	July 24	July 26	July 30	Aug. 15
60.3	July 15	July 20	July 24	July 25	Aug. 1	Aug. 15

Egg.—Light bluish green in color, with a distinct yellowish tinge. Normally stalked, laid singly. Micropyle white; micropylar network pattern indistinct. Length of egg, 0.99 to 1.07 mm., average 1.05 mm.; diameter, 0.46 to 0.5 mm., average 0.49 mm.; length of stalk, 4.49 to 5 mm., average 4.68 mm.

First-instar larva (one day old).—Almost identical with the first-instar larva of *C. oculata*. One large black spot covering dorsum of head; a prominent notch at posterior border, extending nearly to middle. All lateral tubercles except meso- and metathoracic having two prominent setae projecting laterad; meso- and metathoracic lateral tubercles having three setae each; lateral tubercles fairly prominent. Body entirely yellowish gray; a pair of brownish spots in front of mesothoracic depressions; metathoracic tubercles with a large area of basal part brownish, this being the darkest part of the body. First abdominal segment without lateral tubercles; segments 5 to 8 inclusive with brown spots at base of large outer pair of dorsal tubercles; tenth segment with three longitudinal dark lines; dorsal tubercles on segments



CHRYSOPA CHI

1, Mature third-instar larva. 2, Second-instar larva. 3, Normal egg. 4, Cocoon enclosing pupa. 5, First-instar larva. 6, Head and prothorax of adult showing markings. 7, Series from specimens of inter-antennal markings to show gradation from X to Y: 71, a typical X, or C. chi; 72, the sub- and supra-antennal dots are fused with the inter-antennal mark; 73, the separation of these dots has begun; 74, the supra-antennal dots have separated and the sub-antennal dots have retained only a small connection; 75, the sub-antennal dots have become disconnected; 76, a typical Y, or upsilon, variety

(All x about 10¾)

1 to 7 bearing two setae each; dorsal papillae very inconspicuous and having one small seta each. Total length of larva, extended, 2.04 mm.; width at metathorax, 0.76 mm.; width of head, 0.42 mm.

Second-instar larva.—General color gray, with reddish brown or brownish black markings. Head gray, with large, black, undivided patch above. First two lateral thoracic tubercles gray. Prothorax with large, brownish black, dorsal area between depressions. Anterior subsegment of mesothorax gray, crossed by reddish bands; posterior subsegment largely gray, but marked with red; stalks of tubercles white, but with traces of brown in front and behind. Metathoracic tubercles entirely brownish black to velvety black. Basal areas to whitish border of dorsal vessel of each stalk, the same in color, this being the darkest part of the body. First abdominal segment without definite lateral tubercles, but generally with a rounded swelling on each side; these swellings and the tubercles on segments 2 to 4 inclusive, gray; remaining tubercles also gray, but in some cases slightly marked with brown; eighth abdominal segment reddish yellow, with three black lines; ninth and tenth segments pale reddish yellow; lateral setae long, gray in color, six to fourteen from each tubercle; all thoracic papillae and dorsal abdominal tubercles and papillae to fifth segment, gray; on segments 5 to 8, dorsal tubercles black; abdomen with large, triangular, black color patches. All lateral tubercles gray except metathoracic. Total length from tips of jaws to tail, 0.29 mm.; width at metathorax, 1.42 mm.; width of head, 0.64 mm.; length of head and jaws, 0.96 mm.; length of longest thoracic setae, 0.76 mm.

Third-instar larva.—Color dark brownish red, with grayish or yellowish white border. Head with three large black spots above; antennae dark; jaws amber-colored. First subsegment gray. Between prothoracic depressions dark reddish. First two pairs of thoracic tubercles largely white; metathoracic pair dark reddish velvety brown; bases of stalks same color, causing this to be the darkest part of body; an irregular grayish or yellowish area on each side of dorsal vessel on thorax. Abdomen entirely reddish black except dorsal papillae and tubercles, which are yellowish. No lateral tubercles on first abdominal segment. Lateral tubercles back to eighth segment gray or yellowish; a dash of gray extending antero-laterad from each dorsal tubercle, this bar of gray, with the gray along the dorsal vessel and the light borders, being the only light areas on the abdomen. Stalks and bases of lateral tubercles gray or yellowish, forming a light border on each side of the abdomen; irregular paired yellowish marks on highest parts between sutures; setae long, prominent, from twelve to fifteen on each knob; ventral side of abdomen gray; from seventh segment caudad brownish, a pair of triangular brown patches from thorax to seventh segment. Width of head, 0.92 mm.; length of mandibles, 0.88 mm.; width at metathorax, 1.72 mm.; total length of larva, 7.1 mm.; length of longest setae, 1.2 mm.

Pupa.—Cocoon normally elongate spherical, of white, closely woven silk, of the texture of coarse paper; original framework giving it a slightly woolly appearance. Length of cocoon, 3.26 mm.; width, 2.71 mm. (For characters of pupa, see facial and prothoracic characters of adult.)

Adult.—Entire body largely light green in color. Head and thorax prominently marked with jet black; conspicuous Y-shaped mark between antennae; a pair of black spots below bases of antennae, and another pair above. (The inter-antennal spot may be variously connected with these spots, giving a variety of patterns. Frequently the connection is slight.) A large black spot

below each eye, and two small spots near the upper border of each eye; two black spots on outer borders of clypeus; labrum and mouth parts brownish; last segment of palpi banded with black, other segments spotted. Basal segment of antenna green, second segment with a black ring; remainder of antenna brownish. Three pairs of large black spots on pronotum, symmetrically arranged. Mesonotum also with three pairs of black spots, one behind the wings. Wings of moderate length, somewhat acute at tips, hyaline; longitudinal veins green; costal and radial cross-veins mostly blackened at one or both ends; gradate series wholly black; branches of radius black at base; wings as a whole dark. Length of adult, 13 to 16 mm.

(As previously pointed out, a series of six or eight varieties in the interantennal marks exists, but there appears now to be small necessity for their formal designation. Furthermore, there is a marked difference in the coloration of the venter of the abdomen. This is variously marked, from the commoner green to entirely brownish black.)

Chrysopa rufilabris Burmeister (Plate LXXXIII)

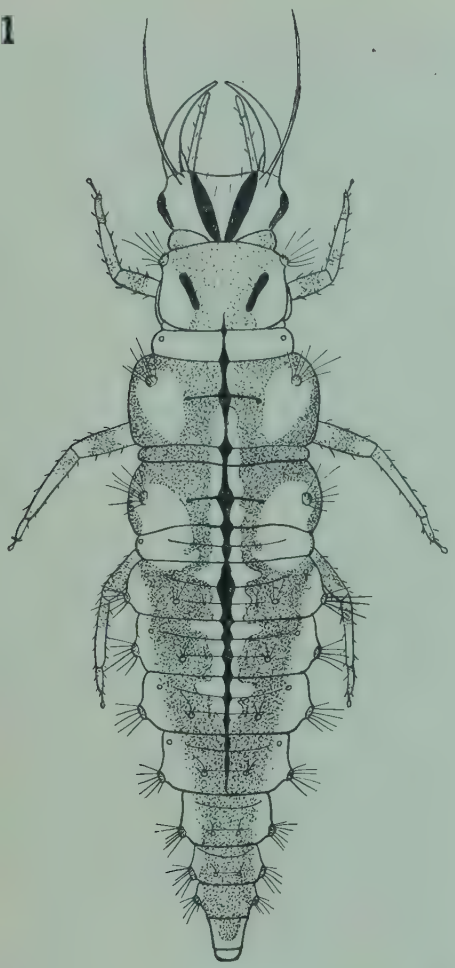
1839 *Chrysopa rufilabris.* Burmeister, Handbuch Ent., vol. 2, p. 979.
1851 *Chrysopa rufilabris.* Schneider, Symb. ad monograph. gen. Chrysopae, p. 79.
1861 *Chrysopa rufilabris.* Hagen, Synopsis Neuroptera N. Amer., p. 219.
1903 *Chrysopa rufilabris.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 152.

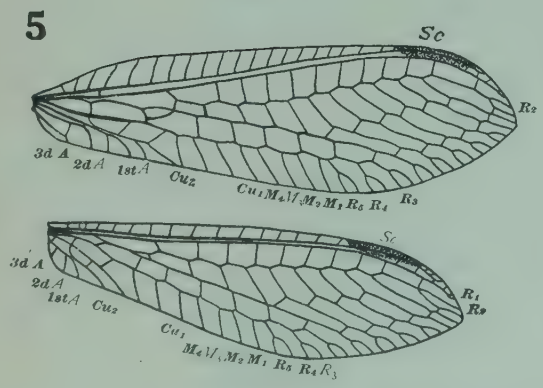
The species *Chrysopa rufilabris* varies considerably and many specimens do not exactly fit descriptions. There appears to be a gradation from *rufilabris* to *interrupta.* In these studies the specific name *interrupta* was applied to very light, "straw yellow" specimens, and *rufilabris* to the darker forms. The latter are by far the most abundant. It is not unlikely that these two species are in reality one, but the writer has not had sufficient material of *interrupta* for study to justify definite conclusions.

C. rufilabris is widespread in its distribution. At Milwaukee, it was the most abundant species at lights. Specimens have been taken at Ithaca at lights, in woods, and in shaded goldenrod patches. At Charlottesville they were most abundant in a dense grove of oak and pine. At Dayton, Ohio, they were taken in a goldenrod patch along a fence in an *oculata* habitat. The species is predominately, however, a woods species.

Egg.—Elongate elliptical, very light green to faint yellowish green in color. Stalked, laid singly on leaves of maple and fruit trees, on grape, and on both trunk and leaves of oak. Length of egg, 0.88 mm.; greatest diameter, 0.48 mm.; length of stalk, 4.0 mm.

First-instar larva.—Head very large, out of proportion to remainder of body; gray, with two broad, longitudinal, convergent, faded black bands on dorsum, arising inside of bases of antennae, and extending posteriorly the entire length of head. Antennae and palpi grayish translucent. First subsegment of prothorax translucent; second subsegment wholly translucent but with pinkish tinge; depressions prominent, dark brown to black. Next two thoracic segments





CHRYSOPA RUFILABRIS

1, Mature third-instar larva, showing color pattern. 2, Mature second-instar larva a few hours before molting. 3, First-instar larva, about midway in the instar. 4, Egg. 5, Wings of adult, x about 3¼. 6, Head and prothorax of adult, showing coloration

(All except No. 5 x about 10¾)

and first eight segments of abdomen having same general pattern; each bearing a pair of prominent lateral gray tubercles and a pair of gray dorso-median tubercles with black tips; ninth segment of abdomen without lateral tubercles; tenth segment cylindrical, dark brownish black; each lateral tubercle bearing two setae except meso- and metathoracic pairs, which bear three each. Dorsal vessel indistinct; general color of dorsum faint pinkish, darker in anterior abdominal region due to food taken in. Legs translucent, with dark smoky areas on distal ends of femora and proximal halves of tibiae; tips of tarsi black. Length of larva, 1.2 mm.; width of head, 0.4 mm.; width at metathorax, 0.36 mm.

Second-instar larva.—Head with two large converging black spots above; jaws dark, tips amber; palpi and jaws with amber tinge. Prothorax with a light yellowish central area, on each side of which is a border of dark reddish brown. All tubercles very small, inconspicuous, white or light yellowish in color; stalks short; setae short. Between prothoracic depressions and extending posteriorly, a dark reddish brown area. Meso- and metathoracic tubercles having prominent yellow areas circling their bases, extending medianly and slightly posteriorly. On each side of the dorsal blood vessel a rather regular pinkish area. Abdomen bordered on each side by a white to yellowish white border, which increases in width to sixth segment; ninth segment with three dark spots above; tenth segment yellowish white. Between yellow side borders of abdomen and yellowish borders of dorsal blood vessel, color dark reddish brown. Legs very dark, blackened near joints.

Third-instar larva.—Head pale yellowish gray, with two longitudinal, jet-black, converging bars on dorsum, these bars pointed anteriorly and broadest at about the middle. First subsegment of prothorax smoky gray in color, crossed by two brick-red dorso-median bands which extend back over second subsegment and converge between its depressions; lateral tubercles and border of segment distinctly yellow. Mesothorax much like prothorax; entire median part a rich, velvety, very dark red; lateral tubercles prominent, wholly yellow, bearing from ten to fifteen colorless setae; a large yellow spot around base of each tubercle, giving segment a prominent yellow border on each side. Metathorax like mesothorax except that the posterior half of the median area is bright reddish while the anterior half is dark velvety red. Abdominal segments all of same general pattern, dorso-median part bright red, darker red outside this area, and yellow border, including lateral tubercles; eight to ten colorless setae from each lateral tubercle, and one or two small setae from two pairs of dorsal papillae on posterior third of each segment; posterior five or six segments darker red than anterior four or five; last segment largely black. Dorsal vessel dark red to black; border very light red, gradually increasing in intensity to dark red of dorso-median part. Venter gray; tubercles yellowish. Length of larva, 7.1 mm.; width at metathorax, 2 mm.

(There is a great variation in the intensity of the reds and yellows of this species in the same locality and in different localities, making this the most puzzling species yet studied. Some larvae are very light and faded, especially near the end of the third instar. In such cases they may show no trace of yellow in the borders, this color being replaced by some shade of gray. In some specimens the head spots extend in a gentle curve, in others they are distinctly angular. The writer has reared some twenty specimens of a species thought to be *C. harrisii*, but the emerging adults were as near *rufilabris* as *harrisii*. These larvae differed from *rufilabris* in having the jaws and the legs quite black, abdominal tubercles 2 to 4 inclusive marked slightly with reddish, and the general body color in some a duller red, and in others, or in different

stages within the instar, a purplish red. The adults had the characters of *harrisii* except that the gradates and a few other veins were partly marked with brown, the wings were less acute than in *harrisii*, and the head coloration was not quite true to description. Knowing the possibility of variations in this species, the writer hesitates to describe it as a new species until further rearing has been done.)

Pupa.—Cocoon silken, oblong spherical, white, closely woven but revealing the pupa within to a greater extent than in any other species seen; outer layer of cocoon fairly coarse, inner layer paper-like. Found commonly on maple leaves. Length of cocoon, 3.26 mm.; width, 3.07 mm. Pupa possessing facial characters of adult; body very light green in color. Total length of pupa, 4.03 mm.; width of abdomen, 7 mm.; length of wing pads, 1.92 mm.

Adult.—Very pale green to yellowish green, with ivory median stripe. Face yellowish white; a faded red stripe from each eye to mouth. Mouth parts and palpi yellowish. Basal joint of antenna yellowish gray, remainder of antenna light brownish. Legs yellowish gray, with a tinge of green in parts. Under side of body yellowish. Wings long, very slender; apex angular; gradate veinlets light brown, costal veinlets brown at ends, many others wholly or in part light brown; longitudinal veins all very light green; veins of hind wings all very light green except gradates and costals. Total length of adult, 14 to 16 mm.

(There is considerable variation in the adult, especially in color shades. The shape of the wings appears to be constant, likewise the brown color of the gradates. The body appears to vary in color from distinctly green to almost gray. The median dorsal stripe varies from yellowish to ivory white. The red stripe from the eyes to the mouth varies from distinct cherry red to pink.)

Chrysopa plorabunda Fitch (fig. 161)

1855 *Chrysopa plorabunda.* Fitch, First report, p. 88.
1861 *Chrysopa plorabunda.* Hagen, Synopsis Neuroptera N. Amer., p. 221.
1903 *Chrysopa plorabunda.* Banks, Trans. Amer. Ent. Soc., vol 29, p. 155.
1907 *Chrysopa plorabunda.* Banks, Cat. neurop. ins., p. 28.

Chrysopa plorabunda was found to be the most abundant species at Manhattan, Kansas, from early spring to late fall. It was found to be especially abundant in summer in alfalfa fields, in corn and sorghum fields, on willow, and on trees on which woolly aphids were plentiful. At Ithaca several specimens thought to be of this species were collected in a strawberry patch near a wood, but they were a darker green than the Kansas specimens. No eggs were deposited. At Charlottesville a third-instar larva was taken in sweeping a clover field on May 17, 1918.

The life history does not differ from those of the *oculata* and *rufilabris* groups. It may be outlined as follows: egg stage, 3 to 5 days; to first molt, 2 to 5 days; to second molt, 3 to 5 days; to spinning, 3 to 8 days; to emergence, 8 to 20 days.

Egg.—Elongate elliptical, light green in color with a decided yellow tinge; stalk hyaline. Stalked as in other species and deposited singly or in irregular groups. Length of egg, 0.87 mm.; greatest diameter, 0.37 mm.; length of stalk, 2.46 to 3.82 mm.

First-instar larva.—Head with two elongate, converging, longitudinal, black bands across dorsum, widening gradually to twice the width toward posterior border. Body predominately gray, with two broken and irregular, brown to reddish brown bands on each side of dorsal vessel, extending full length of body; lateral tubercles small, wholly gray in color, forming gray to yellowish gray border on each side of body. Legs with dark bands distally on femora, proximally and distally on tibiae, and distally on tarsi. Length, 2 mm.; width, 0.5 mm.

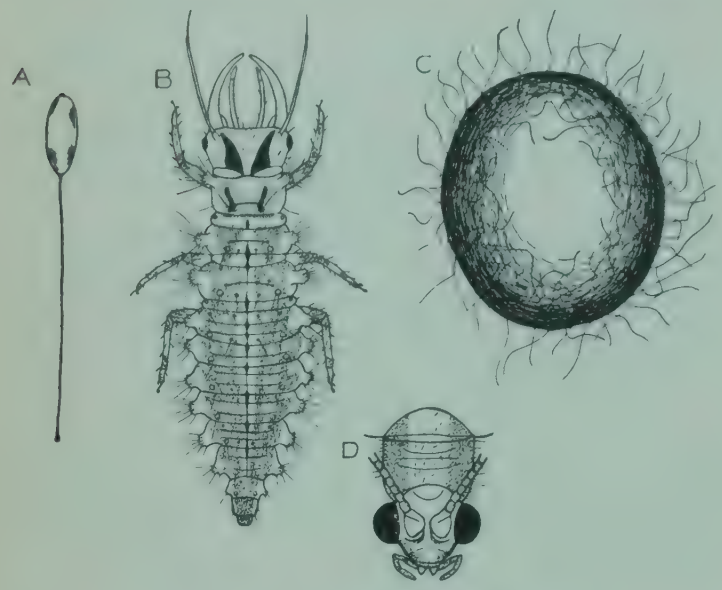


FIG. 161. CHRYSOPA FLORABUNDA

A, Egg, one day after deposition. B, Early third-instar larva. C, Cocoon. D, Cephalic view of head and dorsal view of prothorax of adult
(All x 8)

Second-instar larva.—Same as third instar, except for size. Head gray, with two longitudinal, converging, black or very dark brown stripes above, these broadening abruptly behind,. Thorax and abdomen each with a pair of amber brown or light brown spots, at anterior border on thorax, very irregular and broken up on abdomen; lateral tubercles rather small, wholly gray; eight or more small, colorless setae from each; a gray border on each side of abdomen. Legs dark, a grayish area around middle of femora and tibiae. Length of larva, 5 mm.; width at metathorax, 1.5 mm.

Third-instar larva.—Head predominately gray; two converging black or brownish black bands on dorsum of head, arising at inner side of bases of antennae, widening at base of head; jaws amber; palpi and antennae very light amber; eye spots jet black. Body predominately gray to slight yellowish gray, spotted with light red (near flesh color); anterior thoracic depressions black, each enveloped by a large, elongate, reddish spot; mesothorax with a pair of large triangular spots on each side of dorsal vessel; on remainder of thorax and abdomen, the spotting irregular and much broken up; lateral tubercles medium, wholly yellowish gray, forming a light border on each side of body; setae medium in length, colorless; dorsal papillae and tubercles all gray or yellowish gray; first abdominal segment with very small lateral tubercles, each bearing one or two very small setae. Legs predominately gray; smoky or somewhat blackish areas distally on femora, proximally and distally on tibiae; tarsi predominately black. Venter smoky to yellowish gray, with a reddish border of spots below lateral tubercles. Length of larva, 8 mm.; width, 2 mm.

(This larva resembles that of *C. rufilabris* except that the latter is lighter red in color and its color is more nearly solid. Also the lateral tubercles are smaller in *C. rufilabris*. *C. plorabunda* differs from *C. oculata* in its head markings and in having a complete gray or yellowish gray border to the body.)

Pupa.—Cocoon of white silk, somewhat transparent, almost as much so as in *C. rufilabris*. Length of cocoon, 3 mm.; diameter, 2.75 mm. (Pupae have head and body markings of adult to a large extent.)

Adult.—One of the most beautiful of our lacewings. Body yellowish green (chromium green); head somewhat more yellowish; a prominent greenish yellow (primrose yellow) stripe from head to end of abdomen; wings wholly green; a shining narrow band of reddish black from each eye to mouth; labrum and borders of dark band distinctly reddish.

(This species is distinct, but there appears to be almost a gradation to *C. harrisii*, *C. rufilabris*, and others closely related.)

Chrysopa sp.

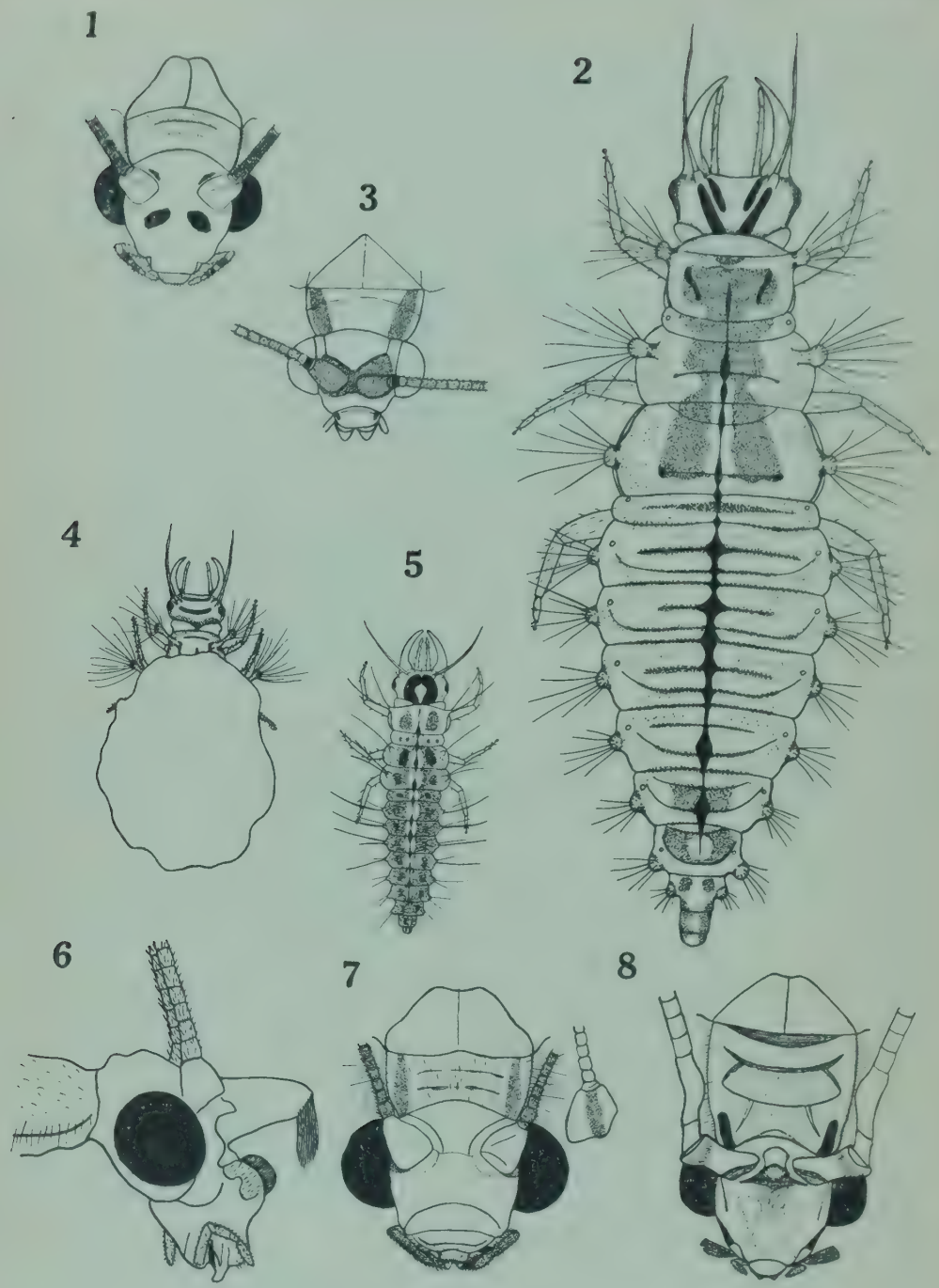
While sweeping goldenrod and asters, and in the Renwick marshes at Ithaca, the writer found two specimens of a gray larva. For some reason they failed to spin but curled up on the bottom of the vial. In a short time both were dead, and so the species is unknown. Since the larva is so distinctive, however, a brief description is included here. Only the third-instar larva was seen. It apparently belongs in the *quadripunctata* group.

Third-instar larva (Plate LXXXIV, 2).—Predominately gray. Head with four elongate black bands on dorsum, converging but not curved, inner pair about half as long and wide as outer pair. Prothorax largely gray; lateral tubercles small, wholly gray. Mesothorax with dark brown to blackish bands on each side of dorsal vessel, extending from prothorax to posterior part of metathorax and forming a saddle-shaped marking. Abdomen wholly gray, somewhat marked with brown or blackish along sutures; first segment without definite lateral tubercles; segments 2 to 5 alike, largely gray, marked with brown in middle and at each side; segments 6 to 8 darker, with prominent brown patches on each side of vessel; segments 9 and 10 still darker; all lateral tubercles relatively small and wholly gray, stalks short.

Chrysopa lineaticornis Fitch (Plate LXXVI, page 1307)

1855 *Chrysopa lineaticornis.* Fitch, First report, p. 91.
1861 *Chrysopa lineaticornis.* Hagen, Synopsis Neuroptera N. Amer., p. 215.
1903 *Chrysopa lineaticornis.* Banks, Trans. Amer. Ent. Soc., vol 29, p. 150.

Larvae of *Chrysopa lineaticornis* have been taken at Ithaca, where they were found on the lower branches and leaves of a linden in a densely shaded locality on August 27, 1916, and following days. Larvae were found also on underbrush near the linden. At Charlottesville, Virginia, they were taken many times during the summers of 1918 and 1919, mostly on the underbrush in woods, on honeysuckle vines, and on



SOME SPECIES OF CHRYSOPA AND MELEOMA

1, Head and prothorax of a female of Meleoma signoretti, x about 10¾
2, Mature larva of an undetermined species, Chrysopa sp. of text
3, Head and prothorax of an imago of a trash-carrying larva from Florida, probably a variety of Chrysopa lateralis
4, Dorsal view of third-instar larva of Chrysopa bimaculata
5, Probable first-instar larva of Meleoma signoretti, x about 10¾
6, Side view of head of male of Meleoma signoretti, showing protuberance, x about 10¾
7, Head and prothorax of Chrysopa lateralis
8, Head and prothorax of Meleoma slossonae, x about 10¾

oak and pine trees. They are readily found, for the little packet of debris moving over a green leaf is rather conspicuous. The best success in finding them was attained on early morning trips, since they appear to be more active at such hours. During the summer of 1918 they were most numerous during the month of September, but in 1919 they were most plentiful in the latter part of July, when all stages of the larvae were readily found. Adults were taken at Charlottesville practically all summer by beating oak branches in rather dense woods. The females have so far uniformly refused to oviposit in captivity. This species was never taken at lights.

Egg.—The egg of *C. lineaticornis* has not yet been seen, but singly deposited eggs of the usual stalked type are common on oak leaves and it is not unlikely that some may be of this species.

First-instar larva.—Conforms to description of third-instar larva except for size, number of setae on lateral tubercles, and dorsal head markings. Four convergent brown bands on dorsum of head; inner pair arising on inner side of antennae at bases of jaws, bending toward each other, and stopping together at about middle of head; outer pair arising between bases of antennae and eyes, extending parallel to inner pair, and stopping at posterior margin of head capsule; bands on posterior part of head, the invaginated part, very faint in color. Body gray, with some brownish or in some cases pinkish markings along sutures and in some specimens on each side of dorsal vessel; these markings, as well as dorsal vessel, inconspicuous; two setae from each lateral tubercle except meso- and metathoracic pairs, which bear three each; stalks of lateral tubercles unusually long. Length of larva, 2.5 mm.; width of head, 0.37 mm.; length of jaws, 0.32 mm.

(All first-instar larvae found, from the earliest to the end of the instar, have a well-defined packet of debris on their backs, identical with that of grown larvae except for size.)

Second-instar larva.—Like third instar with a few exceptions, chiefly as to size. Head grayish, with the two pairs of convergent brown bands as described above, these differing from those in the first instar in that they are broader and their color is a reddish brown, a considerably increased intensity of color; jaws amber, with a reddish brown line on outside of each extending to ocellar fields; a broad reddish brown band from ocellar fields to first subsegment of prothorax, on side of head. Body gray, but with more of the pinkish tinge at sutures and along dorsal vessel, this color being undoubtedly contributed by the viscera of the larva; a distinct brownish patch below each thoracic tubercle and covering proximal ends of coxae. Legs gray except distal ends of tarsi, which are black. Length of larva, 3.5 mm.; width of head, 0.55 mm.; length of jaws, 0.35 mm.

(The packet of debris is likewise a constant characteristic of this instar.)

Third-instar larva.—Head of usual shape, gray in color; two pairs of black or very dark brown bands on dorsum; inner pair arising at bases of jaws and curving toward each other, becoming parallel but not merging, and stopping at middle of head; outer pair arising between bases of antennae and ocellar fields and extending, nearly parallel to inner pair, to posterior side of head capsule, about midway the color becoming less intense and the sides of the bands somewhat irregular. (At the border of the prothorax in this species there is gen-

erally a beginning of a third pair of faint brownish bands, which extend toward the eyes but fuse with the long pair at the posterior end.) Eye spots jet black; jaws amber, with posterior half often dark; palpi and antennae translucent at bases but amber for the greater part. Body predominately gray; anterior subsegment of prothorax lighter gray than dominant color of head; second subsegment light gray in front, light brown behind; lateral tubercles very prominent, knobs at ends small and rounded, stalks unusually long; setae long and prominent, those on thoracic tubercles bending upward and arranged like a horizontal fan to support the packet, whitish to translucent; tubercles all gray. Entire dorsum whitish to delicate gray, main sutures darker. Thorax of normal length. Abdomen contracted and much broader than usual *oculata* type; width equal to that between tips of metathoracic tubercles; first abdominal tubercles not developed; tubercles 2 to 7 small, practically sessile; setae long, the longest ones extending fan-shaped and bending upward; abdominal sutures darkened. Sides of abdomen with a little brown extending full length of body. Tail prominent, somewhat translucent. Venter of thorax grayish to white, occasionally some pinkish due to color of internal tissues. Length of larva, 5.2 mm.; width of head, 0.8 mm.; length of jaws, 0.75 mm.

(All larvae taken have had a well-made packet of the type previously described.)

Pupa.—Cocoon spherical, slightly oblong, entirely of white silk closely woven. Length of cocoon, 3.64 mm.; diameter, 3.07 mm.

(The packet clings to one side of the cocoon and often nearly covers it, the only white silk then showing being on the under side next to the substratum. Larvae may fail to spin, but in such cases they may pupate outside a cocoon.)

Adult.—Specimens reared conform to description given by Banks (1903: 150), with the exception of very slight and probably inconsequential variations in color, largely due to age of specimen.

(Great difficulty was experienced in carrying the pupae through. Of approximately a hundred larvae, not more than a dozen have developed into adults. Midsummer rearings gave some success, but it was evident that the common garden aphids were not their natural food. All attempts at overwintering have failed.)

Chrysopa bimaculata McClendon (Plate LXXXIV)

1901 *Chrysopa bimaculata.* McClendon, Psyche, vol. 9, p. 215.
1903 *Chrysopa bimaculata.* Banks, Trans. Amer. Ent. Soc., vol. 29, p. 153.

Chrysopa bimaculata also is a trash carrier. The only specimens seen by the writer were larvae sent from the citrus groves of Florida through the kindness of Mr. Frank M. O'Byrne, of the Division of Nursery Inspection in the Florida Department of Agriculture. In habits the species is believed to be identical with *C. lateralis* and *C. lineaticornis*, except for distribution. Only the third-instar larva, the pupa, and the adult were seen.

Third-instar larva.—Differs from *C. lineaticornis* in head markings and in size. Head largely gray, with two brownish crossbands on dorsum, a narrow brown band connecting bases of jaws, another similar narrow band connecting

antennae, behind this band two dark brownish irregular patches reaching to prothorax. Body similar to larva of *C. lineaticornis*. Some variation in amount of brownish and black areas, and also in size. Specimens seen apparently on the average a little smaller than *C. lineaticornis*.

Pupa.—Same as in *C. lineaticornis*.

Adult.—Specimens conform to descriptions of type and to that of Banks (1903:153).

Chrysopa lateralis Guér.

Several adults of *Chrysopa lateralis* emerged from larvae sent to the writer from Florida. Unfortunately most of the larvae had spun cocoons by the time they arrived. But on comparing the old head capsule with the larvae that were seen, it appeared reasonably certain that the larvae of *C. lateralis* are almost identical with the same instars of *C. lineaticornis*. The only characteristic observed to be different was in the head markings. *C. lateralis* apparently has the two pairs of dorsal convergent dark brown to black bands. The inner pair arise inside the bases of the antennae, quickly converge, and extend as two convergent bands to a little beyond the middle of the head. The bands are widest in the anterior region and gradually become very narrow at the posterior border. The outer pair arise between the eyes and the bases of the antennae, and extend in a broad curve to the prothorax, almost parallel to the inner pair. On the outside of each of these bands is a large brownish spot of less intensity, making the outer pair of bands appear like a large elongate spot. The other head and body features, as far as known, are the same as are given for *C. lineaticornis*.

From one cocoon there emerged an adult which does not conform to any description yet seen, but it is close to *C. lateralis*. It differs in that the entire first segments of the antennae, and the antennal space on the head, are wholly bright red. But one specimen has yet been seen and there is some possibility that this is a variant.

Chrysopa cockerelli Banks

1903 *Chrysopa cockerelli*. Banks, Trans. Amer. Ent. Soc., vol. 29, p. 154.

About fifty larvae of the species *Chrysopa cockerelli* were first taken on the campus of the Kansas State Agricultural College on October 19, 1921, and following days, on the trunks of maple, linden, and dogwood trees. Several specimens were taken crawling over alfalfa under these trees. These larvae were fed for a time on aphids in the laboratory, but none of them spun cocoons. The larvae were divided into lots and placed in different situations for wintering. The percentage of fatality

was high, but five larvae overwintered successfully. In the summer of 1921, larvae of this species were taken during the latter part of June, early July, September, and October. Adults were taken only once, on August 19, 1921, when they were beaten from willows.

Egg.—All eggs of this species seen were stalked. Average length of five stalks, 4.9 mm. Egg elongate ellipsoidal, light yellowish green in color. Length, 0.8 mm.; greatest width, 0.46 mm. Taken on trunk of maple, June 16, 1921.

First-instar larva.—Head with two pairs of narrow brown bands dorsally; inner pair very narrow, arising at base of mandibles and extending slightly less than half the length of head; outer pair arising at base of antennae, extending posteriorly to prothorax, and doubling anteriorly to eyes; jaws very dark, almost black. Body predominately gray; internal organs visible, causing lighter-appearing areas over body; two setae each from all thoracic and abdominal tubercles except meso- and metathoracic, which bear three each; a row of small hooked setae on dorsum, on each segment from metathoracic to seventh abdominal inclusive. Larva normally carries a small packet of debris, though the usual long stalk of the thoracic tubercles and arched abdomen are not so pronounced as in other instars. Total length, 3.5 mm.; width at metathorax, 0.88 mm.; total length of head and jaws, 0.66 mm.

Second-instar larva.—Differs from third instar chiefly in size. Head and body markings the same as in third instar. Packet present in this instar also.

FIG. 162. FULLY GROWN THIRD-INSTAR LARVA OF CHRYSOPA COCKERELLI, WITH PACKET IN POSITION. DORSAL VIEW. X 10

Third-instar larva (fig. 162).—Head predominately smoky gray dorsally, with three pairs of black bands; inner pair converging behind, almost solid black between them or very dark except for a narrow gray area in middle line; middle pair arising between base of jaws and antennae and extending to prothorax, broadening behind and doubling back to eyes, forming the third pair; jaws amber-colored; antennae almost black, distinctly annulated. Body grayish to white in color, without black markings except along some sutures; prothoracic depressions prominent; lateral thoracic tubercles long and slender; prothoracic tubercles extending forward, setae long, stout, black, with prominent black bases; mesothoracic and metathoracic tubercles smaller and shorter than prothoracic, setae black. Legs very dark, almost black. Abdomen arched, bearing a packet of plant fibers, spider webbing, insect molts, and similar materials; from one to three more or less complete rows of microscopic setae with recurved tip on each segment from the metathoracic to the seventh abdominal segment inclusive; these setae longest on first, fifth, and sixth abdominal segments. Length, 6 mm.; greatest width, 3 mm.

Pupa.—Normally within white silken cocoons, the packet of larva often covering practically all of the cocoon. Pupae have not been found out of doors by the writer. Greatest diameter of cocoon, 2.9 mm.; least diameter, 2.3 mm.

Adult (fig 163).—The adults collected and reared conform rather closely to the original description by Banks (1903), but differ chiefly in the following minor characteristics: head largely ivory-colored, less commonly with a greenish tinge instead of yellowish; black lines to mouth not connecting, though the labrum is light brown; no red on anterior lobes of prothorax; cross-veinlets of wings very dark, the adjacent cells of many appearing smoky nearest the veins; length from head to tips of wings, 10 to 12 mm.

FIG. 163. HEAD AND PROTHORAX OF ADULT OF CHRYSOPA COCKERELLI, X 14

Other trash carriers

From a study of the cocoons in the collection of Chrysopidae in the Museum of Comparative Zoology at Cambridge, the following additional species are apparently trash carriers also: *Allochrysa parvula* Banks and *Leucochrysa floridana* Banks.

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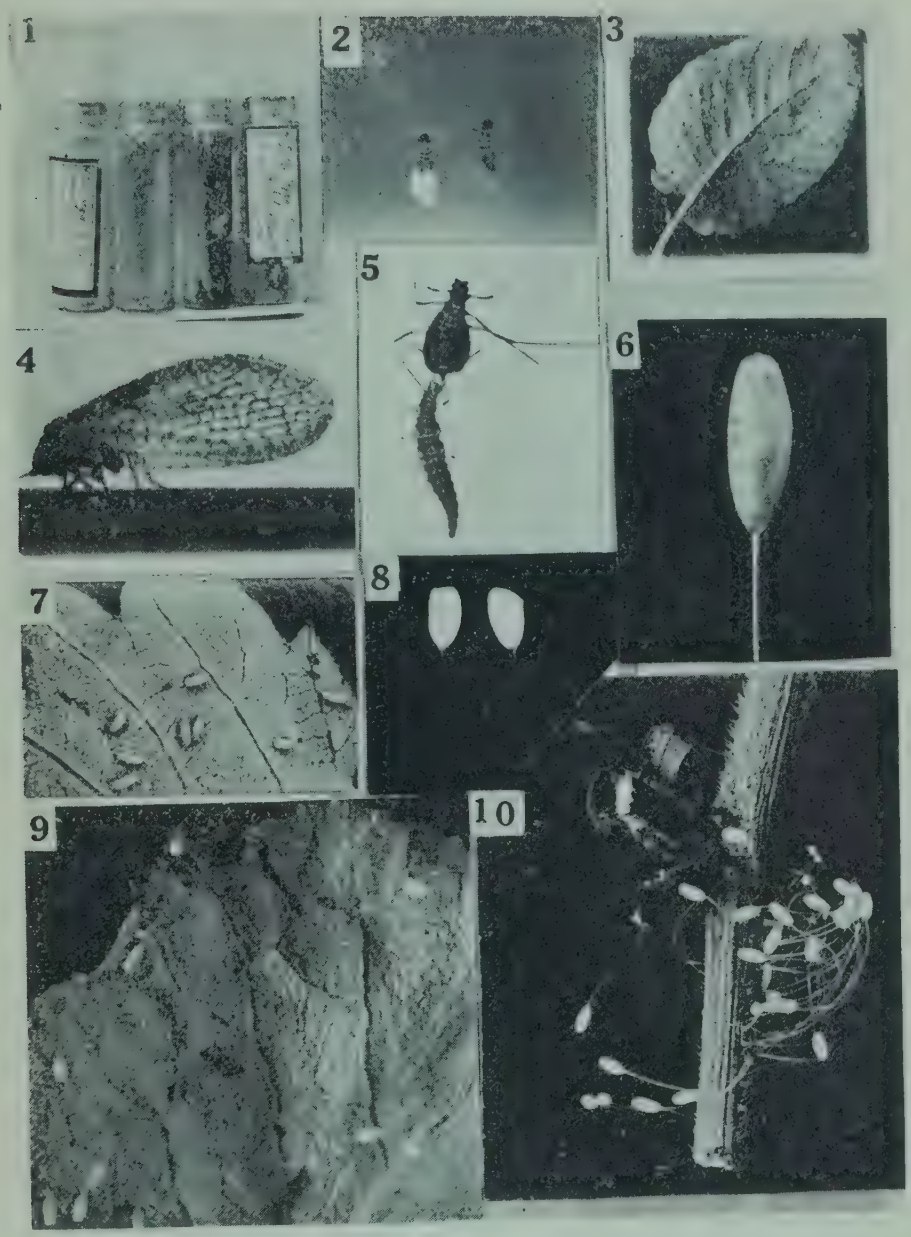
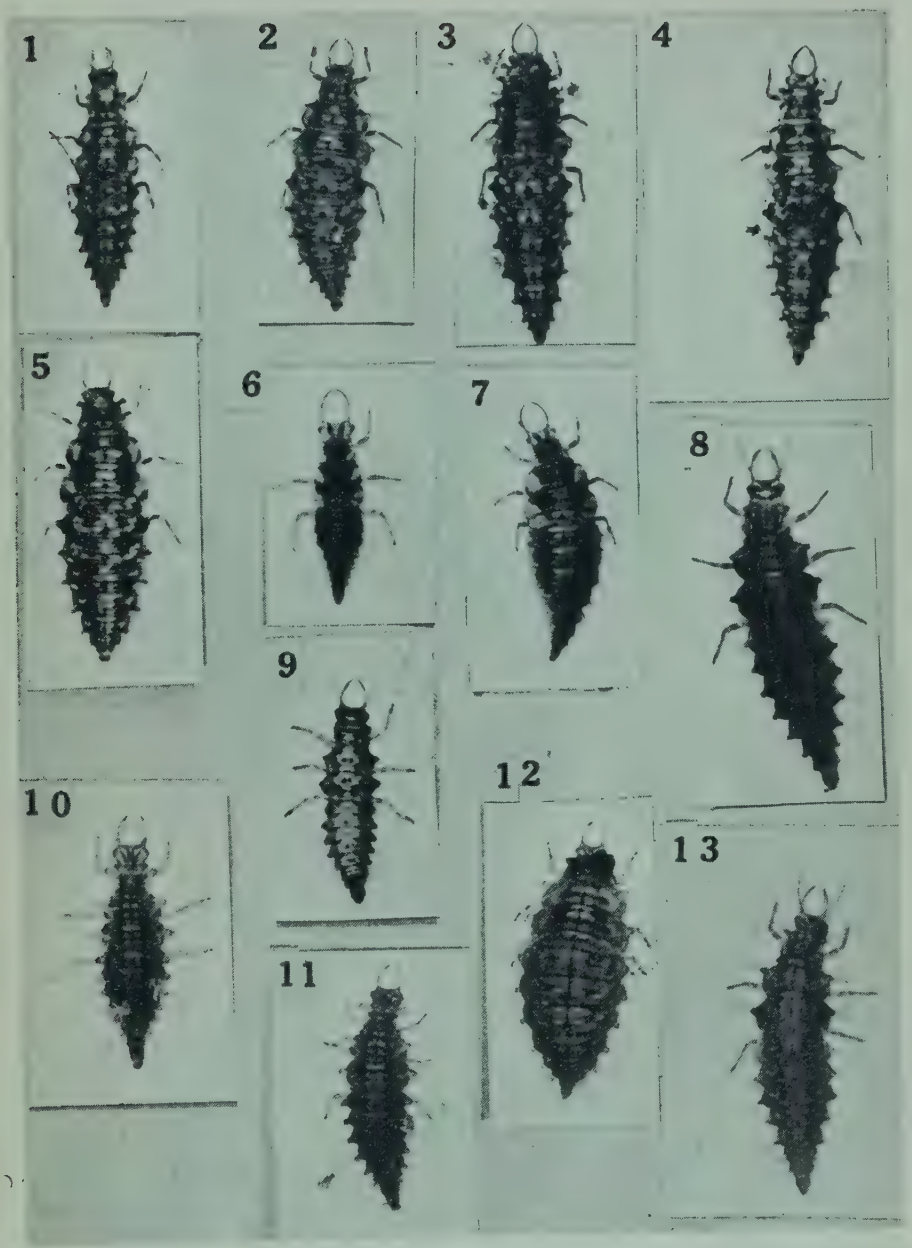


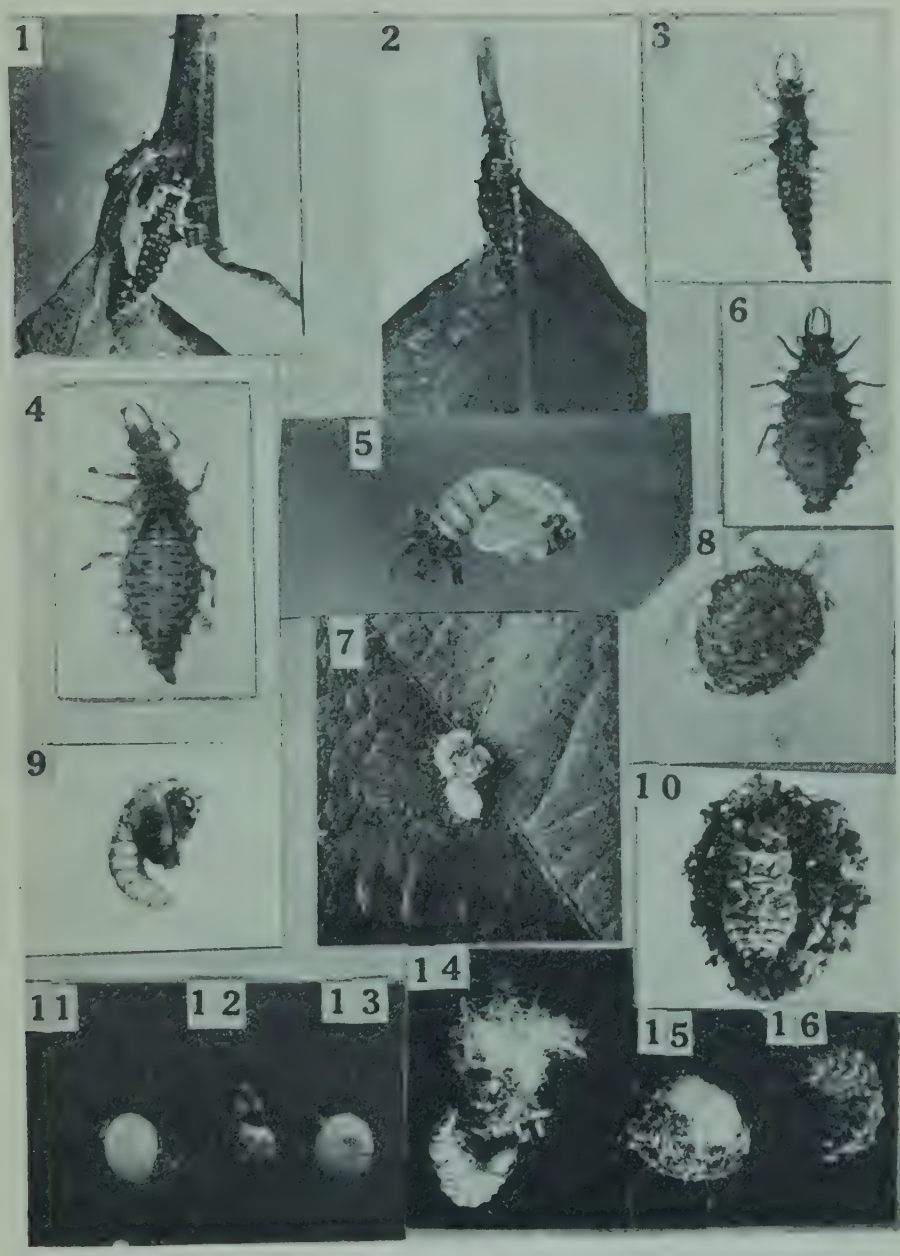
VARIOUS STAGES IN LIFE HISTORY OF SOME CHRYSOPIDS AND HEMEROBIIDS

1, Four dram vials plugged with cotton, as used in these rearings in the study of all stages. The cocoons may be seen
2, A larva of Chrysopa oculata in the final stage of hatching, and a newly hatched larva of the same species
3, Aphids on a leaf of cauliflower, as propagated in the laboratory for feeding chrysopid adults and larvae
4, Adult of a hemerobiid, Micromus posticus Walk., shown for comparison.
5, A grown larva of a hemerobiid, Hemerobius humuli, feeding on an aphid from an aster: shown for comparison with chrysopid larvae; x 3¾
6, An egg of Chrysopa oculata ready to hatch, showing outlines of the embryo: x 9¾. 7, Unstalked eggs of Micromus posticus deposited on a leaf in the laboratory, shown for comparison. 8, Two hatched eggs of Chrysopa nigricornis, showing the rent and the protruding embryonic molt; x 5¼. 9, Hatching eggs of C. oculata on a leaf; one larva may be seen on an egg shell, and others, newly hatched, on the leaf surface. 10, A tangled mass of eggs of C. nigricornis as deposited on a goldenrod stem in the laboratory



LARVAE OF VARIOUS SPECIES

1. Mature second-instar larva of Chrysopa oculata, showing the single head spot. 2, Third-instar larva of C. oculata, mature and about to pupate (the coloration is lighter than the average). 3, Mature third-instar larva of C. oculata with a few aphid skins adhering to lateral setae of thorax
4, Mature third-instar larva of C. oculata var. albicornis
5, Mature third-instar larva of C. oculata var. chlorophana
6, Second-instar larva of C. rufilabris, just molted. 7, Mature third-instar larva of C. rufilabris
8, Early third-instar larva of C. nigricornis, x 5¼
9, Ventral aspect of second-instar larva of C. oculata
10, Early third-instar larva of C. quadripunctata. 11, Grown third-instar larva of C. quadripunctata. 12, Mature larva of C. quadripunctata ready to spin, showing a mass of wax on prothorax from the goldenrod aphids
13, Mature larva of C. nigricornis, to be compared with no. 8
(All except no. 8 x 4½)



CHRYSOPID LARVAE AND PUPAE

1, Early third-instar larva of Chrysopa chi, x 4½. 2, Mature third-instar larva of C. chi. 3, Early third-instar larva of C. chi var. upsilon

4, A larva of unknown identity, designated as Chrysopa sp.

5, Pupa of C. oculata working the old larval skin over the end of the abdomen

6, Mature third-instar larva of C. lineaticornis, with packet of trash removed. 7, Larva of C. lineaticornis on an oak leaf, eating a pine mealy bug. 8, Larva of C. lineaticornis with packet in position; only the jaws of the larva showing.

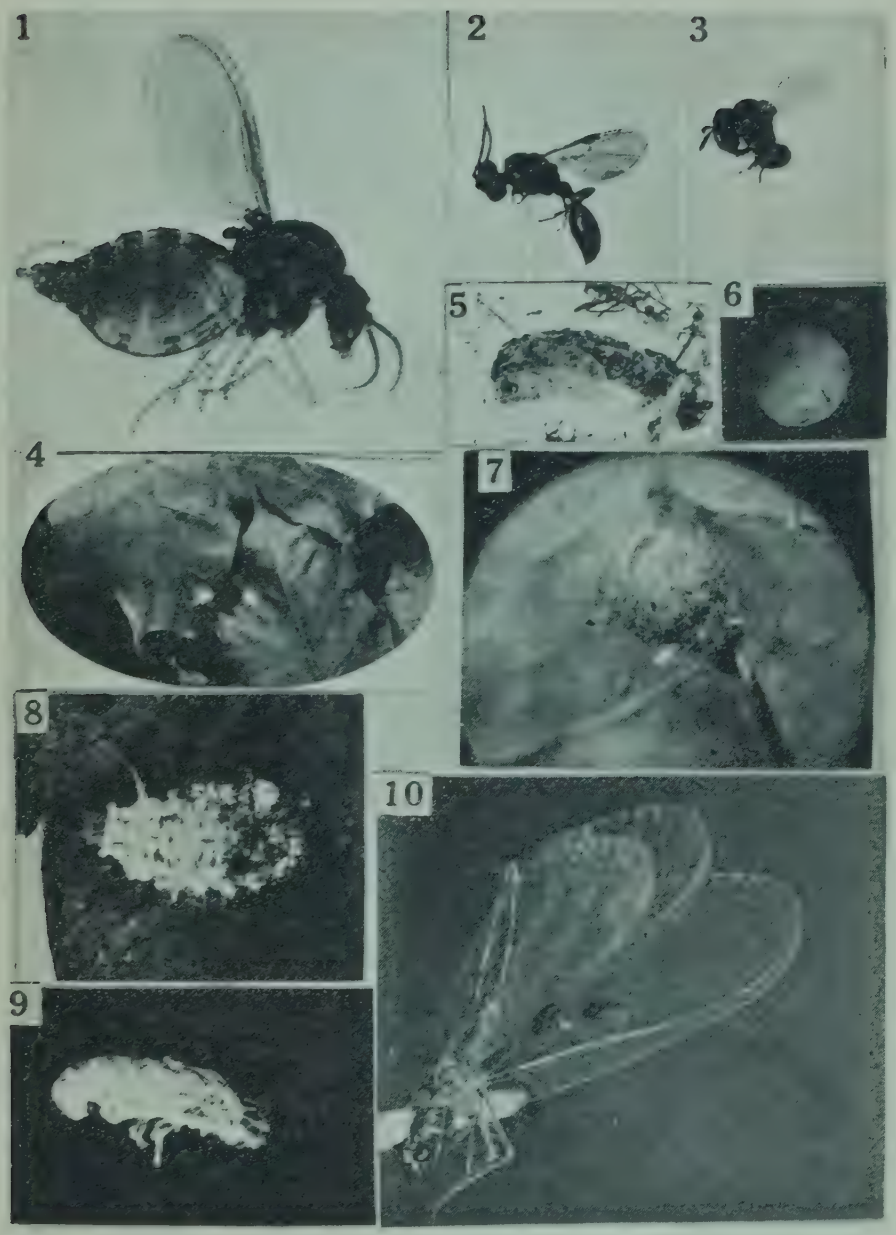
9, Pupa of C. chi in an advanced stage of development

10, Ventral aspect of third-instar larva of C. lineaticornis, showing relation of larva and packet

11, Cocoon of C. oculata, showing lid covering the opening through which the pupa emerged. 12, Pupa of C. oculata leaving cocoon. 13, Cocoon of wintering prepupa of C. oculata, showing flattened area where cocoon pressed against side of vial

14, Prepupa of C. lineaticornis beside larval packet; larva failed to spin a cocoon. 15, Normal cocoon of C. lineaticornis, showing old packet covering a part of cocoon

16, Prepupa of C. oculata, disturbed in spinning, curled up for trans-



VARIOUS STAGES IN LIFE HISTORY OF SOME CHRYSOPIDS AND THEIR PARASITES

1, Photomicrograph of the parasite Pseudoculicoides eques, from a balsam mount

2, Adult of the parasite Hemiteles areator subsp. tenellus, which emerged from a chrysopid cocoon

3, Adult of Perilampus sp., a pupal parasite

4, Cocoons, probably of Chrysopa nigricornis, found on the under side of maple leaves in summer; slightly reduced

5, A normal pupa of a hemerobiid, Micromus posticus, in its cocoon, shown for comparison

6, Wintering cocoon of Chrysopa nigricornis

7, Cocoon, probably of a trash carrier, found on under side of oak leaf at Charlottesville, Virginia, in September, 1918

8, Mature third-instar larva of C. quadripunctata, with trash over the abdomen; x 5¼

9, Pupal molt of C. oculata

10, Adult of C. oculata, with two parasites of the species Pseudoculicoides eques on a wing

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AGRICULTURAL EXPERIMENT STATION

SOME RELATIONS OF ORGANIC MATTER IN SOILS

F. A. CARLSON

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SOME RELATIONS OF ORGANIC MATTER IN SOILS

F. A. Carlson

The effect of lime on the organic matter in soils has been for some time one of the leading problems for investigation. The results that have been recorded, however, are not consistent. Some investigators have reported that there is a greater accumulation of organic matter in limed than in unlimed soil, while others have stated the contrary. This difference of opinion is not surprising when the methods of experimentation, the soil variations, and the climatic conditions are considered. There has been, however, too great a tendency to draw conclusions from unreliable data. In many cases, attempts have been made to study the effect of lime on the organic matter in soils without a knowledge of the composition of the soils before treatment.

In view of the many discrepancies in the reported results, the present experiment was designed to ascertain the effect of lime on the organic matter in soils under various treatments and cropping systems.

HISTORICAL

Wheeler and others (1899)[1] reported that lime decreased the percentage of humus in soils under continuous culture of cereals. They found also that there was an increase of roots and residual organic matter in limed grass plats as compared to those not limed.

Hess (1901) studied the effect of lime on some of the Pennsylvania soils. He stated that liming resulted in a diminution of the nitrogen.

Kossovich and Tretjakov (1902) stated that the addition of calcium carbonate to soil retarded the decomposition of organic matter.

Hartwell and Kellogg (1906) pointed out that the amount of humus in limed plats was less than that in unlimed plats. They stated also that the effect produced by lime upon the organic matter of a given soil was dependable to a considerable extent on the degree of acidity or of alkalinity of the soil.

[1] Dates in parenthesis refer to *References Cited*, page. 25.

Pot experiments by Clausen (1906) conducted with clover and oats on sandy soil indicated that applications of lime resulted in a marked nitrogen hunger, especially during dry, hot weather and with non-leguminous crops.

Van Suchtelen (1910) found in laboratory experiments that soils treated with calcium oxide produced less carbon dioxide than did unlimed soils.

Alway and Trumbull (1910) say:

> In a comparison of 22 rotation plots no distinct relation has been found between the composition of the soil and the nature of the rotation. In a long cultivated field the till was found poorer in humus, nitrogen and organic carbon than the lacustral clay. The amounts of the above three constituents found in any of the plots depend more upon the relative proportions of the two types of soil occurring on the plots than upon the previous treatment.
>
> The longer the fields have been kept in grasses mown for hay, the less has been the change in composition of the soil. Continuous bare cultivation along tree rows has caused greater losses than the alternation of fallow and crop in the adjacent fields. The extreme loss of nitrogen, humus and organic carbon in 25 years is about one-third of the amounts originally present in the prairie.

Bradley (1912) conducted pot experiments from which he pointed out that the nitrogen loss was appreciably reduced by legumes.

Mooers, Hampton, and Hunter (1912) reported that the loss of nitrogen was appreciably greater on limed plats than on unlimed plats, and that the effect extended below the depth of plowing. These investigators stated also that there was an increase in percentage of humus on the unlimed sections.

McIntire (1913) writes:

> Burnt lime decreased the organic matter when applied alone and lessened the accumulation when applied with manure.
>
> Calcium sulphate and ground limestone increased organic matter.
>
> Each form of lime resulted in an increase of nitrogen content, gypsum, limestone, and burnt lime, being effective in the order named.

Lipman and Blair (1913) reported that in their experiments the limed plats had lost nitrogen to a greater extent than had the unlimed plats.

Gardner (1914) says: "Burnt lime appears to exhaust the humus in the soil more rapidly than ground limestone. Burnt lime with manure gave returns over manure alone. . . . It is desirable that the use of lime or limestone lead to larger supplies of organic matter in the soil."

Swanson (1915) reported results based on the chemical analyses of cultivated and uncultivated soils in seven representative counties in Kansas. He pointed out that the elements

carbon and nitrogen have disappeared from the cultivated soils to a larger extent than from the uncultivated soils. He showed that the cultivated soils had lost, in round numbers, from one-fifth to two-fifths of the nitrogen and from one-fourth to one-half of the organic matter.

Potter and Snyder (1916) stated that in a general way the total nitrogen determinations in their experiments showed that there was a smaller loss or a greater gain of nitrogen for the limed soils than for the corresponding unlimed soils.

Bear (1916) indicated that quicklime reduced the amount of carbon and of nitrogen in the soil.

Potter and Snyder, in a later experiment (1917), concluded that lime in the form of a carbonate, under the conditions of the experiment, appreciably enhanced the rate of decomposition of both original soil organic matter and the organic matter of stable manures, oats, and clover when added to the soil. They stated that two of the more important results of this were the increased availability of plant food and the more rapid depletion of the soil organic matter. They pointed out that the latter effect would be partially and perhaps entirely offset by the fact that with lime larger crops could be grown, which would add more organic matter as crop residue to the soil.

Breazeale (1917) found that calcium carbonate had a slight destructive action upon the organic matter of the soil.

Jensen (1918) stated that in most cases when lime was added to alfalfa in basins, greater increase in the humus content occurred than when alfalfa alone was used.

Christie and Martin (1918) state that it is evident from data considered that all soils do not react chemically with lime in the same manner.

Bizzell and Lyon (1918) write: "On Volusia silt loam addition of quicklime increased the amount of carbon dioxide in the soil air. This effect was noticed both on the cropped and uncropped tanks. On Dunkirk clay loam quicklime apparently produced no effect."

Swanson and Latshaw (1919) say:

> In the sub-humid section the fields cropped to grain lost one-fourth of the nitrogen as compared with the surface soil of the native sod. The alfalfa fields contain 5 per cent less nitrogen than the native sod, but 20 per cent more than the fields in grain. . . : .
>
> In the semi-arid section the cropped soil has lost one-fifth of the nitrogen as compared with the native sod. Alfalfa fields contained 15.7 per cent

more nitrogen than the soils in native sod, and 30 per cent more than the soils continuously cropped. . . . .

In the humid section, the cropped soils have lost 36 per cent of the organic carbon present in the virgin sod and those in alfalfa over 21 per cent.

Lipman and Blair (1920 a) summarized a series of experiments as follows:

Lime in the carbonate form was used on a loam soil at the rate of 1 ton per acre for the first 5 years and 2 tons for the second 5 years in a 5-year rotation of corn, oats, wheat and 2 years of timothy. No legume crops were introduced. Twenty plots with different nitrogen treatment were thus limed and twenty similar plots with parallel nitrogen treatment were left without lime.

The total yields of dry matter and of nitrogen for the 10-year period were essentially the same for the two sections.

Analyses of the soil made soon after the work was started and again at the end of each 5-year period showed that there was a loss of nitrogen from both the limed and unlimed sections. However, the loss from the limed section was distinctly greater than from the unlimed section.

Thus at the end of the 10-year period, there was a positive loss rather than gain from the use of lime.

From this work it would appear that the practice of using lime on light to medium heavy soils, *when leguminous crops are not grown* in the rotation, may be questionable. Under such conditions it is quite possible that a slightly acid reaction may be desirable to prevent the too rapid oxidation of organic matter.

The second five-years period showed a distinct loss in carbon from both series, but a greater loss from the limed than from the unlimed plats.

Lipman and Blair (1920 b) reported also a series of experiments which included rotations with legumes. They pointed out that during the ten years, the limed plots, with only slight exceptions, yielded distinctly larger crops and more total nitrogen than did the unlimed plots. In analyzing the soil they found that in a number of cases the limed plots contained more nitrogen than did the unlimed plots.

The same investigators (Lipman and Blair, 1921) reported the results of experiments in studying the losses of nitrogen and organic carbon from a loam soil (in cylinders with natural drainage) which for twenty years had been under a five-years rotation of corn, oats (two years), wheat, and timothy. They found that in most cases there was a general decline in the nitrogen and the organic carbon content. They pointed out that there was a lower nitrogen and organic carbon content in the limed soils than in the unlimed soils. They stated also that the legume green-manure crops tended to raise the nitrogen content.

It is quite impossible to make any direct comparison of

the literature cited, due to the variations in experimental methods and in representation of results. In fact, in many cases there are no data to substantiate the statements made. Furthermore, the making of comparisons of one plot with another on the assumption that the natural variation in fertility is gradual and uniform, is subject to severe criticism. It is likewise impossible to study the effect of lime on organic matter in soils without knowing the original composition of the soils. Also, conclusions drawn from computations based on analyses of soils taken adjacent to plats under treatment and assuming that the results obtained represent the original analyses of the treated plats, are questionable. However, the general conception expressed by the literature is that plats which have been limed contain less organic carbon and less nitrogen than do those which have not been limed. There are some exceptions. This conclusion is based on very limited experimental data.

EXPERIMENTAL

In the present investigation two series of field plats, each 1-100 acre in size, were used. The plats were sampled both before and after treatment. The soil was analyzed for inorganic carbon, organic carbon, and nitrogen.

The soil on these plats consists of glacial material reworked by streams and redeposited from glacial lakes (Lyon and Bizzell, 1918). Owing to its sedimentary origin it is comparatively free from stones. The soil has been classified by the United States Soil Survey as Dunkirk clay loam. It is a heavy, compact soil, and requires careful management. Its average mechanical analysis is as follows:

	First foot (per cent)	Second foot (per cent)
Fine gravel	0.40	0.13
Coarse sand	0.63	0.37
Medium sand	0.83	0.52
Fine sand	1.85	1.05
Very fine sand	12.90	11.27
Silt	60.83	53.95
Clay	22.63	32.72

The following chemical composition was determined by Lyon and Bizzell from representative samples:

Constituents determined	First foot (per cent)	Second foot (per cent)
Nitrogen (N)	0.134	0.062
Organic carbon (C)	1.190	0.300
Calcium oxide (CaO)	0.340	0.280
Magnesium oxide (MgO)	0.350	0.450
Potassium oxide (K_2O)	1.830	2.360
Sodium oxide (Na_2O)	0.860	0.860
Phosphoric anhydride (P_2O_5)	0.084	0.079
Sulfur trioxide (SO_3)	0.084	0.053
Carbon dioxide (CO_2)	0.030	0.020
Lime requirement* (CaO) in parts per million	1,222	1,285
Lime requirement (CaO) in pounds per acre foot†	4,454	4,918

* The Veitch method was used for the determination of lime requirement.
† Calculated from weight of soil as 3,645,000 pounds of dry soil per acre foot in the first foot of soil, and 3,827,500 pounds in the second foot.

SOIL SAMPLING

The plats in Series I were sampled both before and after the ten-years period. Soil samples were taken from each plat to a depth of four feet, each foot being kept separate. Six borings were made on each plat. The borings for the same foot were carefully mixed together and a 2-quart sample of each foot of each plat was retained. The soil samples were air-dried and placed in tightly sealed jars.

The plats in Series II were sampled before and after the eight-years period according to the following method: Each plat was divided into three parts—N (north), M (middle), and S (south). Each one of these sections was sampled as outlined for the plats in Series I.

Preparation of the sample

The air-dried soil was brought to a uniform condition by breaking up the soil lumps and carefully mixing. A composite sample was taken and was placed in a 1-millimeter sieve. All particles of the soil that did not pass through the 1-millimeter perforations were discarded. A composite sample was taken

from the 1-millimeter sample and was passed through a sieve having 100 meshes to an inch. In this case it was necessary to grind the soil in order to pass all of it through the perforations.

In the determinations of carbon the 100-mesh sample was used, while the determinations of nitrogen were made from the 1-millimeter sample. The use of the finer soil in the determination of carbon was based on the uncertainty of obtaining complete combustion with the coarser soil.

The determinations were made in duplicate. All duplicates having a wider discrepancy than 0.02 per cent of carbon and 0.01 per cent of nitrogen were discarded.

Total organic carbon

The total organic carbon was determined by the Parr Combustion Method, as described in Bulletin 107 (revised) of the United States Bureau of Chemistry, page 234.

Total nitrogen

The total nitrogen was determined by the Kjeldahl method. Ten grams of 1-millimeter soil was digested with 30 cubic centimeters of sulfuric acid (specific gravity 1.84) and 0.4 gram of cupric sulfate, in 500-cubic-centimeter Kjeldahl Pyrex flasks at low heat for twenty minutes. Ten grams of potassium sulfate was added and the digestion was continued for three hours. The residue was diluted to 350 cubic centimeters of water and transferred to an 800-cubic-centimeter Kjeldahl flask; from 80 to 90 cubic centimeters of alkali solution was added and the ammonia was distilled into 1-10 N sulfuric acid. The distillate, measuring about 200 cubic centimeters, was titrated with 1-10 N sodium hydroxide, two or three drops of methyl red solution being used as an indicator.

SERIES I

Soil treatment and cropping systems

The plats in Series I were under experimentation for a period of ten years, from 1910 to 1919. A statement of the soil

treatment of each plat, and of the cropping systems, is given in table 1:

TABLE 1. SOIL TREATMENT AND CROPPING SYSTEMS

Plat	Soil treatment		Cropping system
	Fertilizer	Lime	
7002	Farm manure	None	Rotation without legume
7008	Farm manure	Burnt lime	Rotation without legume
7003	Farm manure	None	No vegetation
7009	Farm manure	Burnt lime	No vegetation
7005	Farm manure	None	Rotation with legume
7011	Farm manure	Burnt lime	Rotation with legume
7006	Farm manure	None	Oats, grass nine years
7012	Farm manure	Burnt lime	Oats, grass nine years
7014	Farm manure and K_2SO_4	None	Rotation without legume
7015	Farm manure and K_2SO_4	Burnt lime	Rotation without legume

The applications of farm manure were made in 1910, 1914, and 1918. The three applications were each at the rate of 10 tons per acre, and were given to the plats that were never planted as well as to the cropped plats. The applications of potassium sulfate were made annually to plats 7014 and 7015 at the rate of 200 pounds per acre. In 1910 and 1915 burnt lime was applied to plats 7008, 7009, 7011, 7012, and 7015, at the rate of 3000 pounds per acre.

The rotation without legume consisted of corn, oats, wheat, and grass two years. In the rotation with legume, clover was grown with grass for two years in the first half of the ten-years period, and during the second half of the ten-years period a legume was grown each year as follows: in 1915, soybeans with corn; in 1916, peas with oats; in 1917, vetch with wheat; in 1918 and 1919, clover with grass.

Plats 7003 and 7009 were never planted to any crop, and all vegetation was prevented from growing on them by hoeing.

When corn was growing on the plats in rotation, the unplanted plats were hoed at the same time and in the same way as were the plats planted to corn; when other crops were growing on the planted plats, the unplanted plats were merely scraped with a hoe.

The mixtures of grasses used consisted of timothy, Kentucky blue grass, and redtop.

Results

Organic carbon and total nitrogen in plats before and after treatment

The results recorded in tables 2 and 3 represent the averages of duplicate determinations. The percentages of carbon and nitrogen before and after treatment are given, as well as the differences and the percentage of increase or decrease for the ten-years period. The total amounts of carbon and nitrogen added to the plats in manure, have been subtracted from the amounts of carbon and nitrogen determined on analysis after treatment.

The data show that in the first foot, in every case but one, the limed plats contained more organic carbon than did the unlimed plats. This is very significant in the plats kept in grass. Plat 7012, kept in grass and limed, shows an increase of 20.5 per cent of organic carbon in comparison to an increase of 14.5 per cent in plat 7006, which had the same treatment and cropping except that it was not limed. Plat 7002, cropped in rotation but not limed, shows a decrease of 24.5 per cent of organic carbon in comparison to a loss of 3.1 per cent in plat 7008, which had received lime. This difference is not attributed entirely to the lime. Plat 7002 was exposed to greater erosion and more complete drainage than was plat 7008. All plats in rotation show a decrease in organic carbon in the first foot, while there is a marked gain in organic carbon in the first foot in the plats kept permanently in grass.

The use of legumes in rotation did not materially affect the organic carbon content.

Plat 7009, which was kept bare, lost a marked percentage of organic carbon in the first foot.

The percentages of organic carbon in the second foot are

TABLE 2. PER CENT OF ORGANIC CARBON IN PLATS BEFORE AND AFTER TREATMENT. SERIES 1

Plat	Treatment	Before treatment		After treatment		Difference		Per cent of increase or decrease	
		First foot	Second foot	First foot	Second foot	First foot	Second foot	First foot	Second foot
7002	Crop rotation Manure	1.242	0.536	0.938	0.457	—0.304	—0.079	— 24.5	— 14.7
7008	Crop rotation Manure, lime	1.419	0.545	1.375	0.425	—0.044	—0.120	— 3.1	— 22.0
7003	No vegetation Manure	....	0.420	1.027	0.348	....	—0.072	....	—17.1
7009	No vegetation Manure, lime	1.477	0.470	1.060	0.425	—0.417	—0.045	—28.2	— 9.6
7005	Crop rotation with legume Manure	....	0.420	1.040	0.365	....	—0.055	....	—13.1
7011	Crop rotation with legume Manure, lime	1.470	0.400	1.377	0.428	—0.093	+0.028	— 6.3	+ 7.0
7006	Grass Manure	1.286	0.500	1.473	0.545	+0.187	+0.045	+14.5	+ 9.0
7012	Grass Manure, lime	1.487	0.575	1.792	0.537	+0.305	—0.038	+20.5	— 6.6
7014	Crop rotation Manure, K_2SO_4	1.462	0.497	1.322	0.605	—0.140	+0.108	— 9.6	+21.7
7015	Crop rotation Manure, K_2SO_4, lime	1.405	0.537	1.309	0.528	—0.096	—0.009	— 6.8	— 1.7

TABLE 3. PER CENT OF TOTAL NITROGEN IN PLATS BEFORE AND AFTER TREATMENT. SERIES I

Plat	Treatment	Before treatment		After treatment		Difference		Per cent of increase or decrease	
		First foot	Second foot	First foot	Second foot	First foot	Second foot	First foot	Second foot
7002	Crop rotation Manure	0.123	0.077	0.082	0.056	—0.041	—0.021	—33.3	—27.3
7008	Crop rotation Manure, lime	0.128	0.065	0.118	0.054	—0.010	—0.011	— 7.8	—16.9
7003	No vegetation Manure	....	0.077	0.109	0.057	....	0.020	....	—26.0
7009	No vegetation Manure, lime	0.135	0.070	0.117	0.055	—0.018	—0.015	—13.3	—21.4
7005	Crop rotation with legume Manure	....	0.064	0.115	0.089	....	+0.025	....	+39.1
7011	Crop rotation with legume Manure, lime	0.145	0.069	0.139	0.089	—0.006	+0.020	— 4.1	+29.0
7006	Grass Manure	0.131	0.067	0.137	0.054	+0.006	—0.013	+ 4.6	—19.4
7012	Grass Manure, lime	0.159	0.071	0.161	0.064	+0.002	—0.007	+ 1.2	— 9.9
7014	Crop rotation Manure, K_2SO_4	0.152	0.065	0.125	0.077	—0.027	+0.012	—17.8	+18.5
7015	Crop rotation Manure, K_2SO_4, lime	0.142	0.081	0.125	0.090	—0.017	+0.009	—12.0	+11.1

less consistent than those in the first foot. This inconsistency may be accounted for by lack of soil uniformity.

The limed plats not only contained more organic carbon, but also gave higher yields, than the unlimed plats. The yields are expressed in graph form in figure 1 (page 17).

With one exception there was a greater percentage of nitrogen in the limed plats than in the unlimed plats. The plats in rotation all showed a loss of nitrogen in the first foot for the ten-years period, while the plats in grass increased in nitrogen. Plat 7009, which was kept bare, lost a marked percentage of nitrogen in the first foot. Plat 7011, on which the rotation included legumes, lost a smaller percentage of nitrogen in the first foot than did the plats in rotation without legumes.

These results are consistent with the results obtained on the lysimeter tanks (Lyon and Bizzell, 1918). The soil in the lysimeter tanks was obtained from the plats used in these experiments. It was found that the nitrogen in the drainage water from the lysimeter tanks was less where the tank soils had been kept in grass, than in a rotation. It was shown also that the tank soils kept bare lost more nitrogen than the cropped tank soils.

Ratio of carbon to nitrogen in plats before and after treatment

The ratios of carbon to nitrogen in plats before and after treatment are given in table 4. The data show the close relation between these two elements in the soils studied. The ratio was wider in the first foot of soil than in the second foot. The various treatments did not cause any constant change in the carbon-nitrogen ratio. The effect, if any, was too inconsistent to be considered significant.

The results compare favorably with those obtained by Hess (1901). He found that the ratio of carbon to nitrogen was not materially affected by the treatment applied. Dyer (1902) also reported that the carbon and nitrogen contents of the upper stratum of the soil were higher than those of the lower stratum, and that the ratio of carbon to nitrogen was wider in the upper stratum. Alway and McDole (1916) likewise found that the ratio of carbon to nitrogen was lower in the second foot than in the surface foot.

TABLE 4. RATIOS OF CARBON TO NITROGEN IN PLATS BEFORE AND AFTER TREATMENT. SERIES I

Plat	Treatment	Carbon-nitrogen ratios			
		Before treatment		After treatment	
		First foot	Second foot	First foot	Second foot
7002	Crop rotation Manure	10.1:1	6.9:1	11.4:1	8.2:1
7008	Crop rotation Manure, lime	11.1:1	8.4:1	11.7:1	7.9:1
7003	No vegetation Manure	.....	5.5:1	.....	6.2:1
7009	No vegetation Manure, lime	10.9:1	6.7:1	9.1:1	7.7:1
7005	Crop rotation with legumes Manure	.....	6.6:1	9.0:1	4.1:1
7011	Crop rotation with legumes Manure, lime	10.1:1	5.8:1	9.9:1	4.8:1
7006	Grass Manure	9.8:1	7.5:1	10.7:1	10.1:1
7012	Grass Manure, lime	9.4:1	8.1:1	11.6:1	8.4:1
7014	Crop rotation Manure, K_2SO_4	9.6:1	7.6:1	10.6:1	7.8:1
7015	Crop rotation Manure, K_2SO_4, lime	9.9:1	6.6:1	10.5:1	5.8:1

Removal of nitrogen from the soil in crops grown on the plats in Series I

The amounts of nitrogen removed in the crops were estimated and are recorded in table 5. The nitrogen is expressed in pounds per acre for the ten-years period.

TABLE 5. AMOUNT OF NITROGEN IN CROPS. SERIES I

Plat	Crop	Fertilizer	Burnt lime (pounds)	Nitrogen in crops (pounds per acre, total for ten years)
7002	Rotation without legume	Farm manure	0	684
7008	Rotation without legume	Farm manure	9,000	798
7005	Rotation with legume	Farm manure	0	817
7011	Rotation with legume	Farm manure	9,000	948
7006	Grass	Farm manure	0	325
7012	Grass	Farm manure	9,000	354
7014	Rotation without legume	Farm manure and K_2SO_4	0	844
7015	Rotation without legume	Farm manure and K_2SO_4	9,000	868

It appears that the nitrogen varies with different crops. The greatest removal of nitrogen was in the crops in rotation with legumes. The hay crops removed less than half the amounts of nitrogen estimated in the crops in rotation with legumes. These results are of extreme importance in considering the total nitrogen in the soils of these plats recorded in table 3, in which, as already stated, it is shown that the plats kept in grass increased in nitrogen in the first foot, while the plats in rotation with legumes and those in rotation without legumes decreased in nitrogen. The fact that less nitrogen was removed from the grass plats may aid in some degree in explaining these differences in percentages of nitrogen.

Total yields of crops on plats in Series I

The total yields of crops in Series I are represented in figure 1.

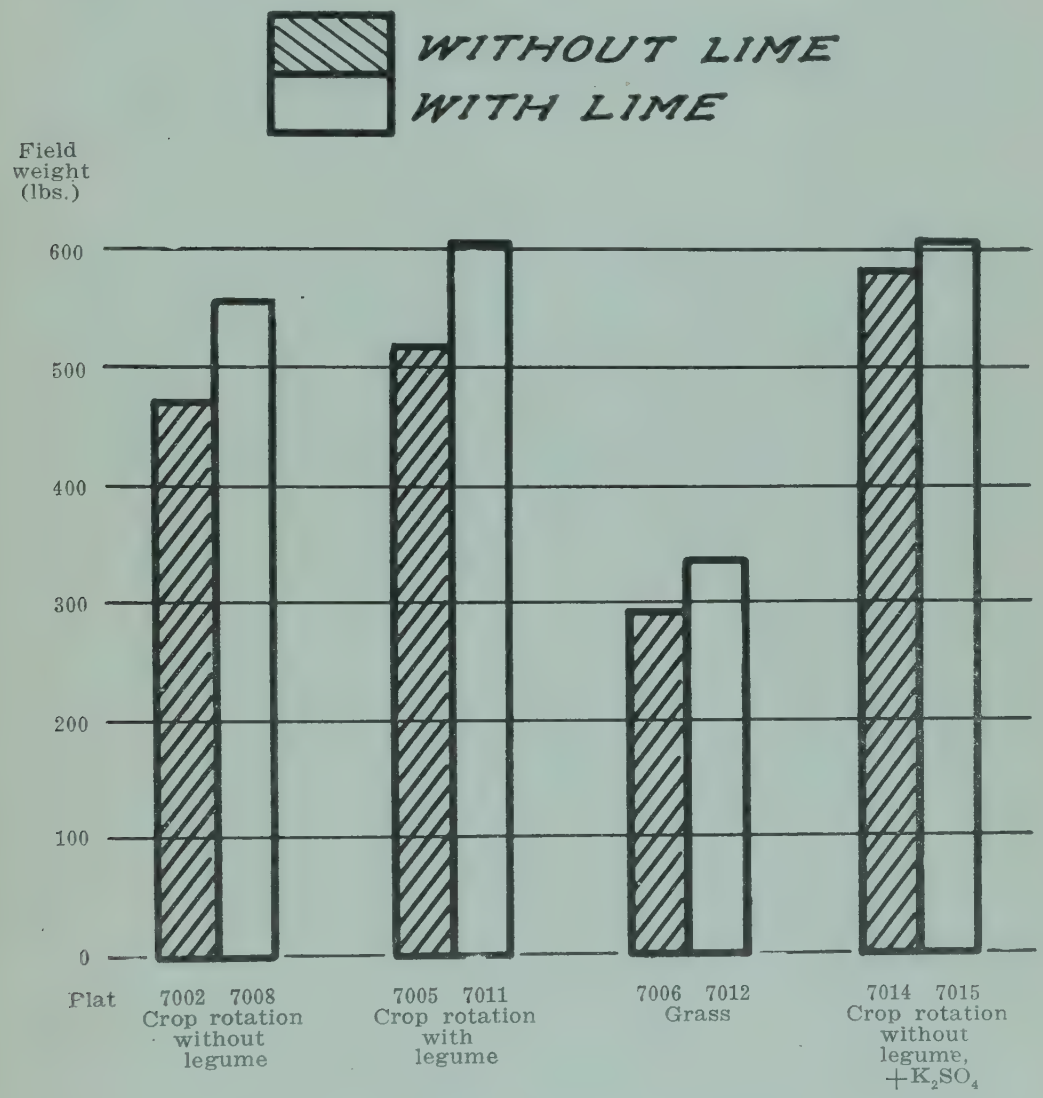

FIG. 1. TOTAL PLAT YIELDS FOR TEN-YEARS PERIODS, SERIES I

In every case there was an increase in crop yield on the limed plats over that on the unlimed plats. It seems logical to

assume that an increase in yield is associated with an increase in roots and residual organic matter, which may explain why the organic carbon and the nitrogen were generally higher in the limed plats than in the unlimed plats.

The total yields were less on the plats kept permanently in grass than on the plats in rotation with legumes or on those in rotation without legumes. It has already been pointed out, in tables 2 and 3, that the plats in rotation lost more organic carbon and nitrogen in the first foot than did the grass plats.

SERIES II

In order to obtain further information on the effect of treatment and cropping on the organic carbon and the nitrogen in soils, the plats in Series II, located adjacent to plats in Series I, were analyzed. These plats, as already stated, received approximately the same treatment as the plats in Series I, the only marked differences being that the plats of Series II were started one year later than the plats of Series I, and that they received only two applications of manure.

Only the first foot was analyzed, due to the failure of the second foot in Series I to show any consistent results of experimental value.

The results obtained are recorded in tables 6, 7, and 8. These tables are not discussed separately, due to their close correlation with the results of Series I.

The points emphasized in discussing the results of Series I may well be applied to Series II. However, the results in Series II are much more striking. The limed plats, as was found in Series I, show in general a higher percentage of organic carbon and of nitrogen than do the unlimed plats. The limed plats also gave higher yields than did the unlimed plats. There was a decrease in organic carbon and in nitrogen in the plats cropped under the rotation without legumes, with one exception.

The most interesting phase of these results is that the plats in rotation with legumes showed an increase in nitrogen. The percentages are very significant. Plats 7205 and 7211, in rotation with legumes, increased 4.2 and 6.7 per cent, respectively, in comparison to plats 7202 and 7208, in rotation without legumes, which decreased in nitrogen 12.2 and 7.1 per cent, respectively.

TABLE 6. PER CENT OF ORGANIC CARBON IN PLATS BEFORE AND AFTER TREATMENT. SERIES II

Plat	Treatment	Before treatment		After treatment		Difference	Per cent of increase or decrease
		First foot		First foot			
		Sections	Average	Sections	Average		
7202	Crop rotation Manure	N 0.923 M 0.891 S 0.901	0.905	0.879 0.796 0.718	0.798	—0.017	—11.8
7208	Crop rotation Manure, lime	N 0.935 M 0.805 S 0.888	0.876	0.921 0.921 0.876	0.906	+0.030	+ 3.4
7203	No vegetation Manure	N 0.755 M 0.789 S 0.775	0.773	0.626 0.556 0.592	0.591	—0.182	—23.5
7209	No vegetation Manure, lime	N 0.797 M 0.788 S 0.731	0.772	0.821 0.719 0.592	0.711	—0.061	— 7.9
7205	Crop rotation with legume Manure	N 1.064 M 0.982 S 0.966	1.004	1.005 1.005 0.938	0.983	—0.021	— 2.1
7211	Crop rotation with legume Manure, lime	N 1.170 M 1.173 S 0.936	1.093	1.162 1.026 0.066	0.751	—0.342	—31.3
7206	Grass Manure	N 1.026 M 0.948 S 1.012	0.995	1.210 1.102 1.156	1.156	+0.161	+16.2
7212	Grass Manure, lime	N 1.088 M 1.080 S 0.874	1.014	1.387 1.228 1.028	1.214	+0.200	+19.7
7214	Crop rotation Manure, K_2SO_4	N 1.173 M 0.996 S 0.911	1.027	1.087 0.960 0.720	0.923	—0.104	—10.1
7215	Crop rotation Manure, K_2SO_4, lime	N 1.084 M 0.879 S 0.908	0.957	1.062 0.860 0.900	0.941	—0.016	— 1.7

TABLE 7. PER CENT OF TOTAL NITROGEN IN PLATS BEFORE AND AFTER TREATMENT. SERIES II

Plat	Treatment	Before treatment		After treatment		Difference	Per cent of increase or decrease
		First foot		First foot			
		Sections	Average	Sections	Average		
7202	Crop rotation Manure	N 0.120 M 0.115 S 0.110	0.115	0.098 0.105 0.099	0.101	—0.014	—12.2
7208	Crop rotation Manure, lime	N 0.120 M 0.112 S 0.103	0.112	0.109 0.109 0.094	0.104	—0.008	— 7.1
7203	No vegetation Manure	N 0.108 M 0.111 S 0.105	0.108	0.090 0.093 0.087	0.090	—0.018	—16.7
7209	No vegetation Manure, lime	N 0.111 M 0.111 S 0.100	0.107	0.099 0.096 0.079	0.091	—0.016	—15.0
7205	Crop rotation with legume Manure	N 0.122 M 0.128 S 0.103	0.118	0.124 0.119 0.126	0.123	+0.005	+ 4.2
7211	Crop rotation with legume Manure, lime	N 0.126 M 0.124 S 0.110	0.120	0.134 0.134 0.117	0.128	+0.008	+ 6.7
7206	Grass Manure	N 0.118 M 0.114 S 0.108	0.113	0.122 0.127 0.118	0.122	+0.009	+ 8.0
7212	Grass Manure, lime	N 0.129 M 0.115 S 0.112	0.119	0.140 0.124 0.112	0.125	+0.006	+ 5.0
7214	Crop rotation Manure, K_2SO_4	N 0.120 M 0.121 S 0.107	0.116	0.119 0.105 0.103	0.109	—0.007	— 6.0
7215	Crop rotation Manure, K_2SO_4, lime	N 0.113 M 0.111 S 0.101	0.108	0.115 0.101 0.105	0.107	—0.001	— 0.9

TABLE 8. RATIOS OF CARBON TO NITROGEN IN PLATS BEFORE AND AFTER TREATMENT. SERIES II, FIRST FOOT OF SOIL

Plat	Treatment	Carbon-nitrogen ratios	
		Before treatment	After treatment
7202	Crop rotation Manure	7.9:1	7.9:1
7208	Crop rotation Manure, lime	7.8:1	8.7:1
7203	No vegetation Manure	7.2:1	6.6:1
7209	No vegetation Manure, lime	7.2:1	7.9:1
7205	Crop rotation with legume Manure	8.5:1	7.9:1
7211	Crop rotation with legume Manure, lime	9.1:1	8.5:1
7206	Grass Manure	8.8:1	9.5:1
7212	Grass Manure, lime	8.2:1	9.7:1
7214	Crop rotation Manure, K_2SO_4	8.9:1	8.5:1
7215	Crop rotation Manure, K_2SO_4, lime	8.9:1	8.8:1

The plats in grass showed a decided increase in organic carbon and in nitrogen.

The carbon-nitrogen ratios were lower than those in Series I.

Removal of nitrogen from the soil in crops grown on the plats in Series II

The amounts of nitrogen removed in the crops grown on the plats of Series II were estimated and are recorded in table 9. The nitrogen is expressed in pounds per acre.

The results compare favorably with those obtained in the study of the plats in Series I. In considering the nitrogen in the soils of the plats in rotation with legumes, as recorded in

TABLE 9. AMOUNT OF NITROGEN IN CROPS. SERIES II

Plat	Crop	Fertilizer	Burnt lime (pounds)	Nitrogen in crops (pounds per acre, total for eight years)
7202	Rotation without legume	Farm manure	0	555
7208	Rotation without legume	Farm manure	9,000	714
7205	Rotation with legume	Farm manure	0	690
7211	Rotation with legume	Farm manure	9,000	892
7206	Grass	Farm manure	0	312
7212	Grass	Farm manure	9,000	397
7214	Rotation without legume	Farm manure and K_2SO_4	0	652
7215	Rotation without legume	Farm manure and K_2SO_4	9,000	703

table 7, and that removed by the crops, the advantage from the growing of legumes is fully substantiated. The crops in rotation with legumes removed more nitrogen than did the crops in rotation without legumes. In this connection it is important to note also in table 7 that the plats in rotation with legumes contained more nitrogen than did the plats in rotation without legumes. While the plats kept in grass contained more nitrogen than did the plats in rotation, there is a marked difference in the amount of nitrogen removed by the hay crop as compared with the crops in rotation with legumes. The results show that the rotation with legumes used in these experiments supplied more nitrogen than did the rotation without legumes or the grass.

Total yields of crops on plats in Series II

The total yields of crops in Series II are represented in figure 2. The limed plats show a greater yield than the unlimed plats. This was true also of the plats in Series I. The total yields

however, of both the limed and the unlimed plats in Series II are less than those in Series I. It may be pointed out here that the plats in Series II contained less organic carbon and nitrogen than the plats in Series I. This may indicate that there is some relation between organic carbon and nitrogen, and yields of crops.

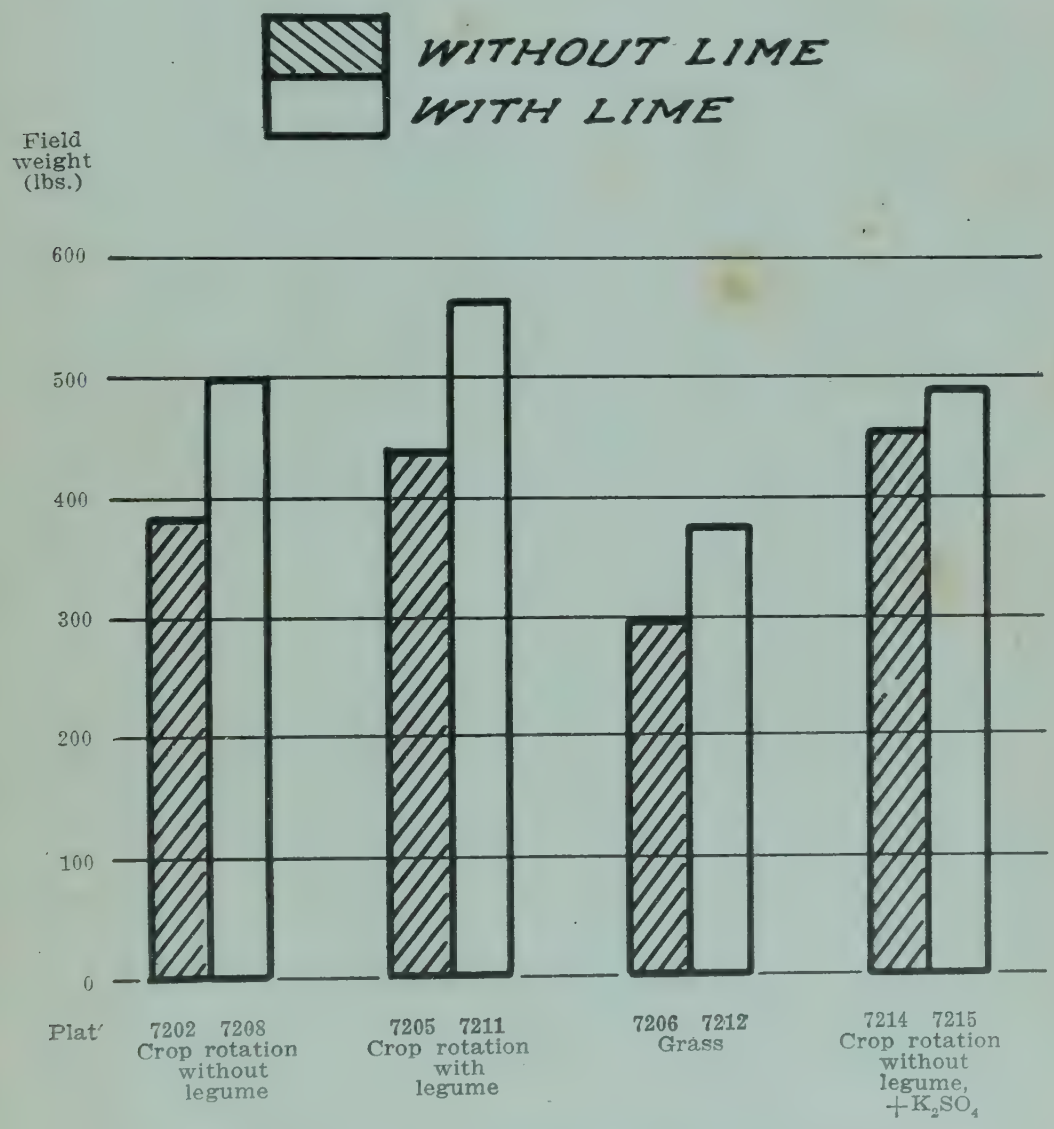

FIG 2. TOTAL PLAT YIELDS FOR EIGHT-YEARS PERIODS, SERIES II

The most important result shown in figures 1 and 2, as related to the present investigation, is the increase in yields of crops on the limed plats over those on the unlimed plats.

SUMMARY

A study of the effect of various treatments and cropping systems on the organic carbon and the nitrogen in soil is reported in this paper. The soil is classified as a Dunkirk clay loam. The plats were each 1/100 of an acre in size and were arranged in two series. The treatments included manure, potassium sulfate, and lime. The cropping consisted of a rotation without legumes, a rotation with legumes, and grass permanently. The experiment was conducted for periods of eight and ten years, respectively.

The plats were sampled for the first- and second-foot strata before and after treatment.

The organic carbon and the nitrogen were determined.

The results of the two series compared favorably.

In general the limed plats in both series contained more organic carbon and nitrogen than did the unlimed plats.

There was a decrease in organic carbon and in nitrogen at the end of the period of experimentation on the plats in rotation without legumes.

The plats kept in grass showed an increase in organic carbon and in nitrogen.

The plats in rotation with legumes contained more nitrogen than did the plats in rotation without legumes. The plats in rotation with legumes in Series II showed a marked increase in nitrogen. The increase was greater in the limed plats than in the unlimed plats. This fact seems to indicate that the legumes had some influence on the nitrogen content of the soil studied.

The organic carbon and the nitrogen were lower in the plats of Series II than in the plats of Series I.

The limed plats produced higher yields of crops than did the unlimed plats.

The plats in Series I gave higher yields of crops than did the plats in Series II.

The results suggest that there is some relation between organic carbon and nitrogen, and yields of crops.

The crops in rotation with legumes removed more nitrogen from the soil than did the crops in rotation without legumes.

The plats kept in grass lost less nitrogen in the crops than did the plats in rotation with legumes.

There is a close relation between the organic carbon and the nitrogen. The ratio is wider in the first foot of soil than in the second foot.

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